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A further study of Dentine

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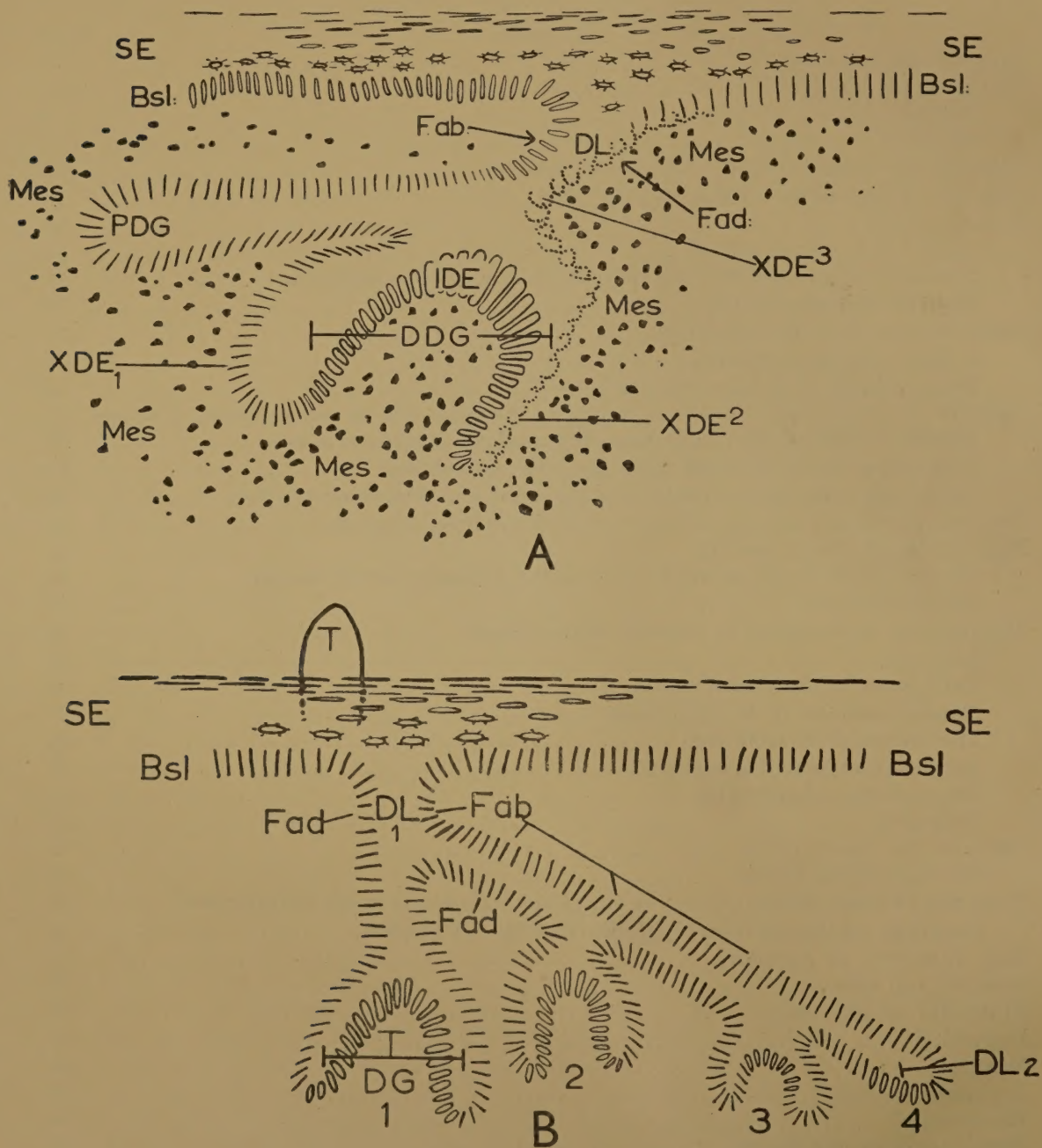
(With 10 plates and 4 figures in the text)

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INTRODUCTION

Dentine is a calcified connective tissue widely distributed among vertebrates. The term originally used for the chief component of a tooth was applied to calcified connective tissues of similar structure. Dentine is present in the teeth of terrestrial and aquatic vertebrates, in the latter it has also a surface distribution in shields, scales and spines particularly in early fossil forms. Dentine wherever situated is a surface structure and teeth are regarded as originating from scales.

Fig. 1.



Diagrams representing the distribution of the DE during the development of teeth.

[See page opposite for explanation.]

Figure 1.

A. Diphyodont vertebrate (based upon a mammal as in Plate 7, figure 4).

B. Polyphyodont vertebrate (based upon an amphibian *Ichthyophis glutinosa*).

They are similar in essential details but in A there are two dentitions only whilst in B there are successional teeth on the DL with constant reformation.

TERMS AND ABBREVIATIONS

1. DE — Dental Epithelium.
 "Dental epithelium", a term introduced by James & Wellings (1943), is used to include all the special cells derived from the surface epithelium which during development determine the form of the teeth and their exact position in relation to one another and to other structures. An objection can be raised that an epithelium is a surface layer of cells either single or stratified. As the dental epithelium maintains a constant relationship with the surface epithelium it emphasizes this important feature and is a useful comprehensive term. The name enamel organ, is so widely employed that its use is likely to continue although the formation of enamel is now known to be relatively a minor function.
2. DG — Dental Germ following the formation of an Enamel Organ (EO) is of the same pattern in all developing teeth.
 A. In a diphyodont dentition.
 DDG for deciduous tooth. PDG for permanent tooth.
 B. In a polyphyodont dentition.
 DG 1. 2. 3. 4. indicate the successional teeth; the elongated cells of 4. are initial to another EO.
3. DL — Dental Lamina.
 With surfaces of Pouchet & Chabry (1884) *F.ad.* (face adamantine) upon which DGs develop and *F.ab.* (face abadamantine) upon which they do not.
 D.L.₁ and D.L.₂ indicate the proximal and distal ends of polyphyodont D.L.
4. IDE — Internal Dental Epithelium (formerly the internal epithelium of the EO) determines the shape of the tooth and initiates the production of dentine.
5. Mes. — Mesenchyme tissues from which the pulp with the odontoblasts forming the dentine and supporting structures and dental tissues, like cementum or bone of attachment, are developed.
6. SE — Surface Epithelium. Bsl.—Basal Layer.
7. T — Indicates an erupted tooth of a polyphyodont. The formed T and successional teeth constitute a dental unit, James & Wellings (1943). All are rarely cut in the same plane of a section.
8. XDE — External dental epithelium (formerly the External epithelium of the EO) determines the position of the tooth. Cuboidal cells becoming polyhedral and forming a network of buds and loops as they proliferate with growth of the DG in A. indicated as XDE. 1. 2. 3. Cells in 1. more or less cuboidal, in 2. more flattened, in 3. the loops should be more spaced where invasion of mesenchyme tissue occurs between cell nodules at a later stage.

All connective tissues are composed of cells and an intercellular ground substance permeated by tissue fluid. The arrangement of the cells during the development of dentine and later in relation to the formed tissue presents special features, for the production of dentine occurs beyond the cells with their intimate blood supply, responsible for its development. Dentine is not truly intercellular as far as the cells that produce it are concerned, in fact at all stages of development and when formed it is acellular and avascular.

The special features recognized in the development of tooth dentine give some idea of the difficulty of coordinating them with our knowledge of the production of other forms of dentine.

The development of tooth-dentine depends upon the differentiation of mesenchyme cells into odontoblasts by the influence of the cells of the internal dental epithelium of the enamel organ (see Fig. 1). The action is attributed to organizers in these cells, and although the nature of "organizers" is at present under criticism von Brunn (1887) recognized the production of dentine as occurring only when internal dental epithelial cells are present. This influence of the I.D.E. has been demonstrated by the growth of dental tooth germs in tissue culture by S. Glasstone (1936) and others. The differentiated mesenchyme cells, as odontoblasts, form a layer beneath the much more distinct layer of internal dental epithelial cells.

The influence of "organizers" in tooth-dentine development has been demonstrated in only a few mammals but, a general application is possible, for such an influence is most probably present in the production of other forms of dentine dependent upon the presence of tubular dentine. This most important relationship is a constant feature in the development of all tissues and has been extensively discussed, Needham (1950), Waddington (1956).

Great advance has been made in knowledge of the ground substance of the connective tissues and when applied to tooth-dentine demands a reconsideration of what is regarded as the normal structure. This applies particularly to the function of the odontoblasts, now regarded as akin to fibroblasts in being fibrogenetic. They are directly connected with the dentine matrix and not with the contents of the dentinal tubules. The collagen fibres completing the walls of the tubules have been mistaken for cytoplasmic processes (Pl. 2, fig. 2 & Pl. 5, fig. 6) and the coagulable tissue fluid contents of the tubules in fixed preparations have been incorrectly regarded as cytoplasmic processes.

These features, upon which a preliminary communication was made to the Anatomical Society, James (1953), provide the basis of the present paper.

This changed conception of tooth-dentine structure is expressed in Text-fig. 2, and is probably true of all forms of tubular dentine.

The present investigation is limited almost entirely to tooth-dentine in view of the new interpretation of its structure and properties. A wide field ranging from the teeth of fishes to mammals has been studied. The tooth tissues in all vertebrates are dependent upon the production of a dental epithelium with an enamel organ for their development and with the exception of group variations the sequence of change is similar. The remarkable resemblance of the cells of

Fig. 2.

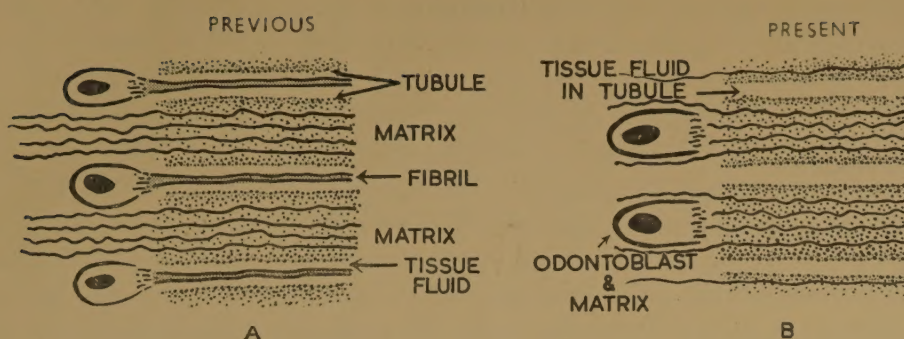


Diagram representing the previous and present interpretations of dentine structure in relation to the odontoblasts. Being in two dimensions the diagram is misleading for the structure represented is a more or less uniform matrix permeated by tubular tapering channels, usually cylindrical in mammals.

PREVIOUS : Odontoblasts with cytoplasmic processes in the dentinal tubules enclosed by the dentine matrix. Tissue fluid is regarded as surrounding the cytoplasmic process in the tubule. The width of the tubule and conception of the other structures are indicated.

PRESENT : Odontoblasts as fibrogenetic cells are directly related to the dentine matrix which is permeated by dentinal tubules containing tissue fluid.

the internal dental epithelial layer of the enamel organs in all vertebrates is astonishing. The similarity is such that it is probable only a most experienced dental histologist although recognizing them as cells of the internal dental epithelium could state to which class of vertebrates they belonged.

MATERIAL AND METHODS

Material.

Sections have been prepared from all classes of vertebrates. These vary in value as the preparation of calcified connective tissues is difficult. Ideal fixation is not always obtained, and if there is an interval after death in specimens not easily acquired, sections are cut although fixation is imperfect. Some animals such as tropical reptiles, demand a temperature for existence favourable to the growth of bacteria and if not fixed immediately are useless. Better sections are usually obtained from small pieces, but derangement of the tissues is frequent when large calcified specimens are reduced to fragments and so rarely attempted. This displacement during cutting of soft tissues in contact with calcified structures is a constant source of difficulty even with well-fixed material; in histological sections the odontoblasts are often pulled away from the dentine during preparation and a difference in density is demonstrated between the softer and harder tissues when they cannot be focused in the same plane.

The head of the specimen, unless very small, is divided in the middle line after the mandible has been separated from the skull. This gives four possible regions with teeth for examination. Serial sections are cut as a routine.

A large number of animals have been examined and those selected for illustration are listed below.

Selected sections illustrated.

MAMMALIA

Human : *Homo sapiens*.
 Chimpanzee : *Pan satyrus*.
 Mangabey Monkey : *Cercocebus*.
 Ring-tailed Lemur : *Lemur catta*.
 Bat : species uncertain.
 Common Shrew : *Sorex araneus*.
 Pigmy Shrew : *Sorex minutus*.
 Lion (foetal) : *Panthera (Leo) leo*.
 Tiger : *Panthera (Tigris) tigris*.
 Cat : *Felis cattus*.
 Brown Bear : *Ursus arctos*.
 Syrian Bear : *Ursus arctos syriacus*.
 Brazilian Otter : *Lutra braziliensis*.
 Guinea Pig : *Cavia porcellus*.
 Hamster : *Cricetus cricetus*.
 Rat : *Rattus rattus*.
 Armadillo : *Euphractus villosus*.
 Two-toed Sloth : *Choloepus didactylus*.
 Three-toed Sloth : *Bradypus tridactylus*.
 Muntjac : *Muntiacus muntjak*.
 Lamb : *Ovis aries*.
 Black Wallaby : *Macropus ualabatus*.

REPTILIA

Agama : *Agama agama*.
 Australian Tiger Snake : *Notechis scutatus*.
 Copperhead : *Ancistrodon contortrix*.
 Gaboon Viper : *Bitis gabonica*.
 Iguana : *Saccodaira pectinata*.
 Puff Adder : *Bitis arietans*.
 Python : *Python molurus*.

AMPHIBIA

American Bullfrog : *Rana catesbiana*.

FISHES

Bowfin : *Amia calva*.
 Cod : *Gadus morrhua*.
 Dogfish : *Scyliorhinus canicula*.
 Grey Gurnard : *Trigla gurnardus*.
 Hake : *Merluccius merluccius*.
 Mackerel : *Scomber scombrus*.
 Minnow : *Phoxinus phoxinus*.
 Mudfish : *Protopterus aethiopicus*.
 Reed Fish : *Calamoichthys calabarica*.
 South American Lungfish : *Lepidosiren paradoxa*.

Fossil sections of " Ordovician Age " (Colorado Bone Bed) from British Museum (Natural History).
 Slides P. 10624 a.b.c.

Methods.

Fixation : formalin 10 per cent was usually used, also formalin 5 per cent, Bouin in different forms, Gilson's fluid and others occasionally.

Decalcification : chiefly with nitric acid 1 per cent or formic acid 5 per cent, Perenyi's fluid is used when the tissues are fixed in Bouin followed by 70 per cent alcohol. X-ray films are taken of all specimens, usually after the jaws have been divided, and further films are obtained to determine satisfactory decalcification.

The plane of a section often difficult to decide upon is helped by obtaining x-ray films, transverse vertical and longitudinal vertical are used as a routine. The curve of the jaw and the positions of the teeth may demand some thought when deciding the exact plane. Sections are often criticized by some workers for not being in the correct plane but as only a few can be exactly central those cut more obliquely, as the majority are in a series, must be accepted and are most informative.

Embedding : the celloidin-paraffin (Peterfi) method gives the best results for the majority of specimens but paraffin or celloidin alone and gelatine used occasionally for frozen sections.

Ground sections with soft tissues present are valuable but rarely sufficiently informative for detail. Fixed specimens are put through the graded solutions of canada balsam then ground and mounted. Sections are examined through degrees of thickness until reduced to a stage giving most information, at approximately 15μ . They are usually difficult to photograph. That occasional sections are good enough for photographing with oil immersion is shown in Pl. 9, fig. 4. Most ground sections are stained in bulk with carbol fuchsin or alcoholic carmine. Also ground sections of dried specimens not previously fixed are prepared.

Microtomes : rotary, rocker, sledge and freezing (gelatine).

Staining methods are systematic. The last of the slides in each tray, the ninth of the series, is stained with haematoxylin and eosin, these are examined and neighbouring sections likely to give the required information are stained, probably two trays, that is eighteen. Variable stains are used in rotation with one in three unstained; Haematoxylin and eosin, Van Gieson, Mallory, Azan, Masson and Silver of which several methods are used and selected unstained slides are given special treatment. All sections in a series are numbered and those not stained are filed and available if needed. The results obtained with a stain can be perplexing, as the same procedure for one animal may not apply equally to another, variation may even be experienced in the same series.

Nearly all illustrations are from photographs taken by the writer, but three (low power) are by Mr. M. Sawyers, namely, Three-toed Sloth, Hake and Pygmy Shrew; the coloured photographs of Rat, Mangabey Monkey and Guinea Pig are by Mr. P. Runicles and a photograph of Human by Mr. E. B. Brain of Birmingham. The whole field other than the part especially focused is often imperfect so that many photographs only show one area in detail. Coloured filters were used but many taken without. The amount of light is controlled by a graded resistance coil.

DENTINE AND OTHER CALCIFIED CONNECTIVE TISSUES

The greatly increased knowledge of the chemical and physical properties of the connective tissues brings them closer together and increases the importance of their histological features. These common attributes apply to the calcified tissues, for instance it is remarkable that a component such as calcium phosphate is present in all as an apatite in relation to the collagen fibres, Bourne (1956).

Dentine being acellular and avascular is structurally in contrast with skeletal bone with blood vessels and cells in Haversian systems. Varying forms of calcified connective tissue range between these extreme types. On the one hand there are structures closely related to tubular dentine* with differences as seen in other forms of dentine, scales, carapaces or shields with some blood vessels and cells. On the other hand there are dermal bones of fishes and of other vertebrates possessing few cells and devoid of blood vessels when in a thin layer.

C. Tomes (1923, p. 276) says: "Professor Kölliker has shown that in a very large number of fishes the skeleton more nearly resembles dentine than true bone in its structure".

Knowledge of the calcified connective tissues is best obtained from their development. Development of tooth-dentine is the main source of information upon dentine, while of bone that of mammals is best known.

The extremes, from dentine and dermal bones to skeletal bone with muscles attached, are equivalent to the distinction between the exoskeleton and the endoskeleton of palaeontologists and anatomists. Dentine is the most superficial of the calcified mesenchymal tissues (Pl. 9, fig. 5), it may be connected with the deeper cellular and vascular calcified structures as in scales Williamson (1849-50). The relationship of these layers is discussed more recently by Moy-Thomas (1939). Enamel, the most superficial calcified structure, should, if present, be regarded as ectodermal however complicated the blending of it with the mesenchymal structures may be † (see Pl. 10, fig. 8).

Interpretation of the differently distributed dentines is difficult, for they vary widely in range and are greatly contrasted by different observers. A dental surgeon, as a clinician, examining tooth-dentine as a calcified connective tissue considers it from its development and as a vulnerable formed structure; whilst the palaeontologist examining tissues in a fossil, regards dentine as a calcified tissue permeated by fine radiating tubules and devoid of cells and blood vessels.

DENTINE OF STRUCTURES OTHER THAN OF TEETH

The distinction between dentine of teeth and of other forms is not at all clear. Tooth-dentine has been extensively studied while other forms have received much less attention.

* Many names have been used for tooth-dentine. "Tubular" used for mammalian teeth is most commonly employed and probably most suitable. Romer has suggested "compact dentine", "hard" and "unvascular" are used. "Ortho-dentine" introduced by Charles Tomes is used by Mummery and others. In the opinion of the writer tubular-dentine should be restricted to dentine dependent for its production upon the influence of the I.D.E. and is the form that precedes all other forms of dentine.

† Reference is made to the careful work of Kvam (1950) who in the opinion of the writer has regrettably introduced the term "mesoderm enamel".

Palaeontologists are restricted to ground sections for the histological examination of fossil material (Pl. 1). Goodrich (1909), a zoologist interested in fossil animals is constantly referred to, he gives a description clearly based upon tooth-dentine : "Dentine differs from bone not only in that it contains no cells but also in that it grows on one surface only, the surface next to the dentinal pulp," how far this applies to other dentine structures is not stated. The common tendency is to assume that all dentines are similar.

The wide distribution of dentine is expressed by Romer (1946, p. 10) :

"In dermal bones and scales the deeper layers usually consist of characteristic bone, arranged in laminae ; the middle portion in fishes presents a spongy appearance due to the presence of numerous blood vessels. The superficial layers vary greatly. Usually, however, bone cells are absent, and the material is a hard compact tissue more or less comparable to the dentine which forms the main bulk of the teeth. The surface of fish scales and head plates is frequently finished by a layer of hard shiny enamel, or enamel-like material, such as covers the teeth. Frequently, the surface of bony plates and scales of fishes shows an ornamentation of tubercles or ridges of dentine and enamel. These superficial structures seem comparable to the dermal denticles which are found in the skin of sharks and to the teeth which are present in jawed vertebrates. The spines often present on the fins of lower fish groups are characteristically formed of dentine and enamel, or similar materials."

Such a generalised statement evokes many questions. How closely do the structures called dentine and enamel in fossil material compare with the tissues of recent animals ? Denticles on the surface of a shield is the most probable interpretation of the sections prepared at the British Museum (Natural History) Smith Woodward (1921) of fossil material from the Ordovician Colorado fish bed (Pl. 1). These are the earliest known vertebrates approximately 400,000,000 years ago. Bryant (1936) described them and in several of his figures indicates the presence of dentine and enamel. The first account of these vertebrates is by Walcott (1892). What preceded the production of structures so highly complex is unknown.

The relation of denticles to dermal bone needs to be studied more fully. Goodrich (1909, p. 66) says :

"Thanks to the researches of Williamson (1849-50) *, Leydig (1894-5), Gegenbauer (1872-98) and more especially Hertwig (1874), the ontogenetic and phylogenetic connection of the dermal bones with denticles, like those developed in the skin of Elasmobranch fish, has been traced. Williamson considered that the plates and scales of fish were formed by the combination of superficial denticles with underlying dermal bone. Hertwig supposed that by the enlargement of the basal plate, whereby the hollow tooth-like denticle is fixed in the dermis, or by the fusion of the adjacent basal plates, such superficial bones are developed as are found covering the skull or the roof of the mouth in the lower Gnathostomes."

"Now Hertwig contended that true dermal bones can always be traced back in the lower forms to the denticles from which they were derived ; even when in the higher vertebrates such bones have sunk below the skin, and become closely united to the endoskeleton. Further, that dermal bones always lie outside the perichondrium, and may cover the cartilage bones ; and that cartilage-bones can never be traced back to denticles, and are developed entirely in direct relation to the cartilaginous skeleton."

Although these statements are criticized by recent authorities they represent in a degree the extent of our present knowledge.

* The dates of the references have been added and so are not in order.

The tissues to which the name dentine is applied need to be more clearly defined. When used without a qualifying adjective dentine is the acellular and avascular form commonly called tubular dentine. Special forms of dentine are known as osteo-dentine, trabecular dentine, plici-dentine, vaso-dentine. Component arrangements are described such as mantel-dentine, circumpulpar dentine and other structural features. Early authorities, Hertwig (1874), Charles Tomes (1896) and Rose (1898) described and expressed opinions upon the different forms. Tomes (1898) introduced the names commonly used in Great Britain. Orvig (1951) reduces several named forms to an osteo-dentine group. Kvam (1953) has especially studied enamel referring to its relation to dentine, and Casier (1947-49) has investigated the roots of the teeth of the Euselachii and fossil Pristidae. The nature of the calcified tissues in fossils may become more definite, as the presence of bone in the cephalaspids has been demonstrated by Stensio (1927), and the relations of bone and dentine are considered by Gross (1953), White (1935), Peyer (1937), Moy-Thomas (1939) and others.

The interpretation of the structure of the earliest vertebrates is based on the conformation and detailed arrangement of the calcified fossil connective tissues. For a fuller knowledge a comparison needs to be made with living animals where the soft tissues can be examined, but is not exactly possible as counterparts of the earliest state are not known. Prior to animals with calcified structures those with soft tissues only must have existed, and, except as casts are unlikely to be preserved. Unfortunately fossils of young animals being frail and imperfectly formed are rare, for much might be learnt from them. This limitation of material gives great importance to the structures that were calcified. The endoskeleton, providing the supporting framework to which muscles are attached, is in contrast with the exoskeleton, which is protective and gives the outward form of what is known of the animal. Although they are blended during the process of evolution, as a general conception the endoskeleton is formed of skeletal bone, which is cellular and vascular with muscular attachments, and the protective exoskeleton of dermal bone grading to dentine, which is acellular and avascular. All dentines wherever situated are related to the exoskeleton.

TOOTH-DENTINE

Tooth-dentine is a tissue showing a great contrast between a developing stage with the full activity of well nourished productive cells, and a terminal formed acellular and avascular calcified matrix almost without metabolic changes. Few formed structures have more reduced metabolic demands than dentine, which as a formed structure has been much studied but its tissue fluid has been little considered.

The following definition of dentine would probably be generally accepted: "Dentine is a highly elastic calcified connective tissue devoid of cells and blood vessels with a laminated matrix, composed largely of collagen fibres and mucopolysaccharides, permeated by tissue fluid in spaces or tubules radiating from the surface of its development".

The definition is the stage at which most comparisons with other structures are made. In fact a formed tissue with fine tubules permeating an acellular calcified matrix would usually be called dentine. Such a description would apply to a vertebrate's tooth (Pl. 3, fig. 9), certain parts of the scales of a fish (Pl. 9, fig. 5) or the "bony" shield of fossil fish (Pl. 1, figs. 1-4). The dentinal tubules on the outer part of the scale of *Latimera* are clearly shown by Roux (1942). Dentine is also shown in sections of the exoskeletons of the Osteostraci, Denison (1951).

Detailed studies of human teeth on account of pathological lesions have been made by dental surgeons and much of our information is based upon these investigations. A closer study of the soft tissues in their relation to the calcified structures is needed, for often dried specimens alone are examined by zoologists, and with fossil material the absent soft tissues should be constantly kept in mind. This applies not only to the different dentines but to all the calcified connective tissues for a nearer correlation of these tissues is possible it now being recognized they possess common attributes in a greater degree than formerly.

Dentine as a tooth component.

Superficially all teeth consist of two parts, a crown which projects and is free, and a root* or base attached to the supporting structures. It is surprising that although these external characters of a tooth are so marked, dentine, the essential component, does not show a distinction between crown and root, nor are they defined in the pulp. Dentine is formed first and other calcified dental tissues subsequently added.

When compared there is a great contrast between the conical form of the root of a mammalian tooth and the tooth with an open base of other vertebrate classes. In a dried specimen of a tooth with an open base the pulp surface of the dentine is exposed, whereas the mammalian tooth needs to be split for dentine to be seen and under ordinary circumstances is exposed only by wear from functional usage.

In diphyodonts, tubular dentine surrounds the pulp, but in polyphyodonts only caps the pulp.

Contrast between the teeth of polyphyodont and diphyodont dentitions.

A rarely emphasized but very important difference in arrangement of the tissues is seen in the animals grouped as polyphyodonts and diphyodonts (Figs. 1 & 3). The successional teeth of polyphyodonts are usually of short duration and have an open base that becomes ankylosed or firmly attached to the subjacent bone, whilst diphyodonts have teeth with contracted roots attached by fibres to the bone

* Root is here used for the part of the tooth that becomes attached to the supporting tissues. The crown is the free part of a tooth. The neck is at the junction of the root and crown to which the subgingival epithelium is attached, James & Counsell (1927). Some authorities confine the term "root" to the teeth of the contracted form but as it is not universally accepted the above may seem desirable. Jenkins (1950) is correct in saying of the teeth of fishes: "These teeth have not roots like those of higher vertebrates". Casier (1947, 1949) uses root for the attached part of the tooth with an open base. Root of a tooth however used is not likely to be misunderstood if it is recognized as the attached part.

forming a socket, and have a dentition lasting the life of the animal, called permanent, succeeding a milk or temporary dentition. The molars of the permanent dentition do not have predecessors and are regarded by some authorities as of the milk dentition.

Although the contrast in the disposition of the completed tissues in polyphyodonts and diphyodonts is so marked, the initiation and continued development of the tubular dentine in both forms has a similarity, in that the conical root closes only as the tooth is established in its final position. The end of the embedded part of the completed tooth is usually the widest in polyphyodonts and the narrowest in diphyodonts.

Fig. 3.

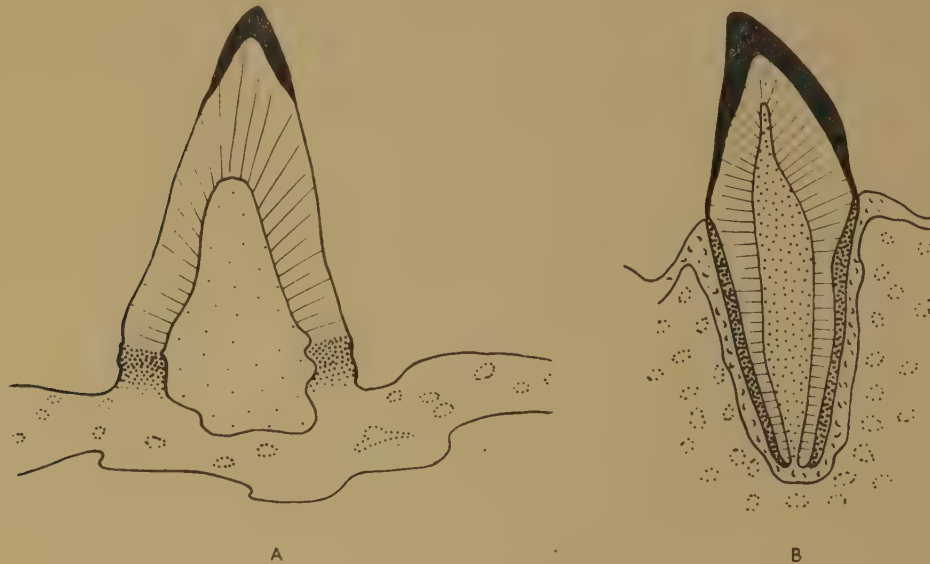


Diagram indicating the mode of attachment and the arrangement of the tissues.

A. Polyphyodont tooth with a wide open base.

B. Diphyodont tooth with a contracted root.

The black cap is enamel in a diphyodont mammal and in some other vertebrates but of an uncertain nature in many polyphyodont fishes. Lines indicate dentine. The polyphyodont tooth (A) is connected to the bone by fibres or a bone of attachment (shown by black dots).

The diphyodont (B) has a bony socket to which the root of the tooth through cementum (black dots) is connected by the periodontal membrane (short lines) outside the cementum to the bone (dotted rings). Pulp is shown by open spaced dots. The periodontal membrane is continuous with the dermis of the mucous membrane.

This distinction between these two types is associated with the completion of development of the tubular dentine. Further production cannot occur upon the teeth with an open base when the bone of attachment or another kind of dentine is formed upon it; whilst in the contracted root form, development of the tubular dentine continues until the root termination is completed down to an apical foramen. In most mammals cementum is added externally as the root develops. It is also well seen in the crocodile. The crown may have enamel or a kindred tissue upon its outer surface and when first exposed a cellular layer is present.

The diphyodont dentition is mainly confined to mammals and the polyphyodont to reptiles, amphibians and teleost fishes.

Hinge teeth are present in many predatory teleost fishes, they have an open base in direct relation to the bone supporting them like ankylosed teeth.

The teeth of the elasmobranch fishes with fibrous attachment only to their supporting structures do not belong to either group, and although polyphyodont, the root is not widely open, and trabecular dentine is formed upon the tubular dentine. That they approximate more closely in their form to the diphyodonts than other polyphyodonts is of interest as are the special features present in their development and mode of eruption, James (1953).

In some fishes, as in the Dipnoi (Pl. 9, figs. 1, 7), the bulk of the tooth may be nearer to dermal bone than to dentine in structure. Despite the wide range of animals and the varieties of tooth forms presented, the general structure of the dentine throughout is remarkably similar.

Structure of Tubular Dentine.

Tubular dentine, the foundation tissue upon which all teeth are built, consists of a matrix permeated by spaces or tubules. The presence of tissue fluid in the tubules is recognized but cytoplasmic processes from the odontoblasts cannot be demonstrated. The tubules usually have an empty appearance, particularly beyond the area of development a feature so characteristic that dentine is recognized by it (see Pl. 3, figs. 4, 7, 8, 9, 10, Pl. 4, fig. 4, and others). It is concluded, the generally accepted interpretation of such long standing, that the fibrils of Tomes in the dentinal tubules are cytoplasmic processes from the odontoblasts, is incorrect. As a structure cytoplasm is not easily defined.

Fluids can pass along the dentinal tubules of a tooth in a living animal or in the dried state. This is shown experimentally by the penetration of dyes in the teeth of mammals, Tomes (1856), Caush (1904-5), Beust (1912), Fish (1932), MacGregor and others discussed by Leicester (1949, p. 236).

The opinions expressed by many authorities upon dentine structure are restricted to human material, although reference is made to other mammals, their conclusions are for the most part assumed to apply to the dentine of all classes of vertebrates, perhaps with some justification in view of the astonishing similarity in development and characters of all enamel organs (see Text-fig. 1).

The close resemblance of formed dentine is seen in highly magnified *ground* sections from the teeth of man, an armadillo and a gaboon viper (Pl. 3, figs. 1, 2, 3). Bryant (1936) already quoted describes dentine, his illustrations (Pl. IX and others) show the tubular arrangement. He draws attention to the absence of cell spaces. Tubules in sections also from the Ordovician Colorado bone bed are shown in Pl. 1 (Brit. Mus. sections P. 10624 a. b. c.) Smith Woodward (1921).

In contrast to the study of macroscopic material, as already mentioned a knowledge of dentine is best acquired by a study of its phases of development, but many young specimens are difficult or almost impossible to obtain. Sections of the teeth in vertebrates with a diphyodont dentition need to be examined in a sequence of ages, but many polyphyodont animals with successional teeth may show several

stages of development in one series of sections. The initial development of a dental lamina is seen only at the earliest stages in the life of most vertebrates and then not infrequently with an enamel organ embedded in the surface epithelium demanding interpretation.

Knowledge of the development of dentine in most forms other than of teeth hardly exists, the general assumption, being that all are similar. The development of the teeth of fossil animals can be inferred only by comparison with living species. The fossils studied are chiefly premammalian and unfortunately in this connection so much of our present knowledge depends upon investigations of mammalian material.

The changed conception of tooth dentine expressed by the writer (see Text-fig. 2. p. 5) invites a full discussion of the previous interpretations of histological appearances.

OPINIONS UPON DENTINE STRUCTURE

J. Tomes and other authorities.

Processes or fibrils described as occupying the dentinal tubules are called "dentinal fibrils" or Tomes' fibres, and are thought by most observers to come from the odontoblasts. Tomes (1856) in his paper "On the Presence of fibrils of soft tissue in the dentinal tubules" does not relate them to the odontoblasts, for his only comment upon the relationship of the fibrils to these cells is contained in the following extract :

"If a *fibril* be examined in its natural condition, by the aid of an eighth of an inch object glass, it will be found to consist of an almost structureless tissue, transparent and of comparatively low refractive power. In glycerine the fibrils are scarcely visible. *At present it admits of doubt whether they are tubular or solid.* In some cases there is an appearance of tubularity ; but being *cylindrical* this may be mere optical effect . . . *The manner in which the dentinal fibrillae terminate in the pulp, I am at present unable to decide.* In favourable specimens they may be traced a short distance into the pulp, but whether they are terminated by cells or in any way connect themselves with nerves, I am unable to determine". (The italics are mine.)

The presence of "soft tissues" in the dentinal tubes recognized by Tomes has been subsequently supported by innumerable authorities, but the latter have described them as processes from the odontoblasts, claiming a connection, and have called them "Tomes' fibres" or "fibrils" although not assumed by him. Tomes examining human dentine, being chiefly concerned with the significance of the fibrils in the relation to tooth sensation says :

"The foregoing observations will I think warrant the conclusion, that the dentinal fibrils are subservient to sensation in the dentine, and are the channels by which nutrition is carried to that tissue."

This view upon sensation is held by recent authorities.

Maximov & Bloom (1952), and Orban (1944, p. 136) writing on the function of the odontoblasts says : "Doubtless they play a part in the nutrition and sensitivity of the dentine and also in the formation of the matrix".

Tomes (1856) remarks :

"When these investigations were commenced, I had but little expectation of finding that one of the most important parts in dental structure had been overlooked, namely, that each dentinal tube is permanently tenanted by a soft fibril, which, after passing from the pulp into the tubes, follows their ramifications."

In coming to this conclusion, the conduction of sensation by the fibril was no doubt in his mind, and the opinions he expressed may account for the views that have become current. If it were possible to interpret his thoughts they would suggest the fibrils are of the nature of nerve fibres.

A few years later Tomes (1859) says :

“ M. Lent (1855) described a series of delicate processes extending from the peripheral cells of the dentinal pulp. He regards them as the organs by which the dentinal tubes are formed, and, like the latter, they divide and anatomose together.” and that Kölliker confirms Lent’s observations.

Howard Mummery and the established views.

Howard Mummery (1892) summarizing views held up to 1891 draws conclusions of particular interest :

“ In this rapidly growing portion of a tooth (Pl. 36, fig. 2) the odontoblast cells are seen to be disposed in a single layer, to lie *square* against the layer of stained uncalcified matrix substance (Pl. 37 b) which is here very broad, and to be distinctly separated from one another . The slight *separation between the odontoblasts*, I have found to be very constant in young dentine. The distinct reticulum of fine fibres is seen *passing between and enveloping the odontoblasts*, and by careful focusing on the right plane (see Pl. 38, fig. 3 e) these fibres can be seen to be gathered into *bundles and incorporated with the matrix substance* out of which they appear to spring.” (The italics are mine.)

He is controverting the opinion then held that the dentine is a homogeneous substance.

Hopewell-Smith (1903) gives the current opinions held at the beginning of this century which are approximately the views expressed in the present-day textbooks :

“ The channel, in the fresh state, contains the dentinal fibril which in transverse sections appears like a delicate roundish dot. This does not necessarily occupy the centre of the canal, although it is most probable that during life it fills, or very nearly fills, its entire length. It is impossible to prepare, for histological purposes, sections of the hard and soft tissues of teeth in combination, without altering their normal characteristics. Hence it seems reasonable to believe that not only does the protoplasmic filament traverse the tube from pulp to extremity but that also it rarely, if ever, completely occludes it.” And : “ it is evident that the contents of the tubules are protoplasmic processes or fibrils which emanate from the odontoblasts of the pulp ”.

But eleven years earlier Mummery (1892) had expressed doubts in the following statement :

“ . . . Further investigation into the contents of the dentinal tubules seems called for ; indeed, the usually accepted view of the origin of the fibril has not appeared satisfactory to all observers. Professor Klein (1879) says : However great the authorities who maintain that the cells of the outer stratum above referred to as the odontoblasts proper, send processes into the dentinal canals as the dentinal fibres, I must question the accuracy of this assertion for I cannot find convincing evidence of those odontoblasts doing more than producing the dentine matrix . . . the dentinal fibres appear to be derived solely from the deeper layer of cells which are wedged in between the former.”

Excepting Mummery and Klein no other authorities express doubt of the presence of cytoplasmic processes from the odontoblasts in the tubules but Klein attributes the “ fibrils ” to deeper cells of the pulp.

THE ABSENCE OF CYTOPLASMIC PROCESSES FROM THE ODONTOBLASTS IN
THE DENTINAL TUBULES

That cytoplasmic processes from the odontoblasts are present in the tubules is stated in text-books and papers but none of the innumerable illustrations in the books and papers clearly demonstrate a connection between an odontoblast and a dentinal fibril.

Odontoblasts in relation to formed dentine terminate with square ends against the matrix, the marked contrast is due to the difference in staining (Pl. 4, figs. 1, 2, 3, 4, and others). This appearance was recognized by Mummery (1892). The tubules are continuous with the intercellular spaces between the odontoblasts and other pulp cells.

One illustration purporting to show odontoblasts with processes passing into the tubules, is figured by Hanazawa (1917, fig. 21). It is a highly magnified section and the processes from the cells marked as dentinal fibrils are characteristic of collagen fibres passing into the matrix.

In Orban (1944, fig. 72) the cells are present and also the tubules passing to the intercellular spaces, some are marked "Dentinal (Tomes') fibers". In Tomes' "Dental Anatomy" (1923, fig. 53), the magnification is too low for determination of the nature of the fibres and many other examples in the literature might be cited that are equally indefinite. In some recent papers indications of Tomes' fibres are made with the electron microscope but these at present are insufficiently clear as to their nature and exact position, see quotations page 21 and D. B. Scott (1953).

Cultures of tooth germs are of particular interest, for illustrations show both odontoblasts and the developing dentine in one section, Glasstone (1936, fig. 6) and Lefkowitz, Mardfin & Bodecker (1954, fig. 7); the connection of the odontoblast with the matrix can be seen and the tubules have the usual "empty" appearance.

It is difficult to believe the tubules of the irregularly arranged dentine seen in pathological specimens as in odontomes or in specimens such as those recently demonstrated by Martin Rushton (1955 & 1956) could depend upon cytoplasmic processes from odontoblasts for their development or formed state.

Absence of processes from odontoblasts in the tubules of prepared sections.

Histological preparations do not support the commonly accepted view that cytoplasmic processes from the odontoblasts are present in the dentinal tubules or spaces, for the odontoblasts are directly related to the matrix both of forming and formed dentine. When seen under a high power objective the continuity is such that it is difficult to say where the cell ends and the matrix commences (Pl. 3, fig. 10, Pl. 4, figs. 5, 7, 8, Pl. 5, fig. 1 and others). The absence of cytoplasmic processes is evident from the characteristic empty or clear appearance of the dentine tubules and their direct communication with the intercellular tissue fluid spaces of the pulp (Pl. 3, figs. 4, 5, 7, 8, 9, Pl. 5, fig. 6, Pl. 7, figs. 3, 6, and others). This empty appearance of the tubules and the absence of cells is diagnostic of dentine.

The contents of the tubules vary between a gel state of larger particles and the more frequent sol or fluid state in the finer channels with little staining properties.

Many authorities attach much importance to the staining properties of the tissues. Certain differences are recognized and can be relied upon, but the degree of development gives rise to considerable variations. As an example, Kramer & Little (1953) say that collagen and reticulin have little in common, for collagen fibres when first laid down conform in all respects to the histological definition of reticulin, and comment upon whether there is a chemical change in argyrophil reticular fibres to non-argyrophil collagen fibres. The greater amount of carbohydrate in reticulin is a possible explanation. The remarkable imperfectly stained dentine of the Dipnoi, *Protopterus* and *Lepidosiren*, may be due to the presence of reticular fibres. (Pl. 9, figs. 6 & 1.)

Similar explanations may apply when using stains regarded as selective in which granules that might be regarded as cytoplasm are red and precollagenous green or blue. The figures in Pl. 2 are reproductions in approximate colours of sections with Masson and Azan stains. The appearances presented show the association of fibres and granules related to the odontoblasts and their connection with the predentine and dentine. Such sections are interpreted as showing cytoplasmic processes passing to the tubules. Staining of the tissues differ according to the dyes used, but commonly, as in these sections, the odontoblasts are red with strands crossing the predentine layer that are fibrous and granular and also stained red. They appear more fibrous with a low power objective but more granular with a higher power (Pl. 2, figs. 1, 2). Possibly cytoplasmic cones project from the odontoblasts, but they continue as collagen fibres to the matrix of the formed dentine. These fibres are seen as a constant feature *passing to the wall of the dentinal tubule and continuing production of the matrix*. The end of the developing matrix has a rounded appearance (Pl. 5, fig. 3) upon which formation continues. The fibres passing to the wall of a tubule have been regarded as entering the tubules (Pl. 5, fig. 6). The red stained processes or granules (Pl. 2, figs. 1 & 2) are green or blue in precollagenous filaments, and like the red fibres are arranged vertically in the forming predentine to the dentine matrix beyond. These granules undergo a similar change to collagen fibres and the formation of the dentine matrix as seen with the red fibres formed as projections from the odontoblasts.

It would seem that where the odontoblasts and predentine are sufficiently firmly held by "red stained" fibres connecting them to the dentine that they remain in position when fixed, in contrast with those usually pulled apart in preparation. The relationship of these granules and fibres to the odontoblasts and the forming dentine is a constant feature in the development of tooth-dentine. The red fibres projecting from the short processes of cell cytoplasm have the appearance of coming directly from the cell, (Pl. 2, fig. 3) thought many years ago to be the explanation of the formation of white connective tissue fibres from a fibroblast. The production of collagen fibres by odontoblasts is discussed later (p. 24). Examination of Pl. 2, figs. 1, 2 with a hand lens shows the granular nature of the elements forming the predentine and can be recognized as directly associated with the odontoblasts.

Although valuable, Azan, Masson and Mallory as differential stains are difficult to interpret with differences in reaction seen even in the same series of sections.

The fixative may be a factor but there are other features needing explanation. Cytoplasm as a living part of the cell is not easily distinguished from the products of its activity, as is well demonstrated in the continuity of the granules in an odontoblast with those of the dentine matrix (Pl. 4, figs. 5, 6, 7, 8). Stains with better known chemical and physical properties may become established.

That there is a greater extension of the cell cytoplasm in fishes is possible, as suggested to me by Dr. T. Kerr who is investigating the so-called enamel or vitro-dentine of elasmobranchs. Kerr (1955) inclines to the view that there are cytoplasmic extensions well beyond the cell, basing his opinion upon the staining reaction with Masson when both the cell cytoplasm and the projecting "fibre" stain red.

The pointed extension of the cytoplasm as seen in the dogfish and the continuity of the cell with the matrix (Pl. 7, fig. 8), is in contrast with squared ends of the odontoblasts joining the matrix in mammals, but as seen in this figure the fibres beyond the cell have the appearance of collagen fibres and the granular cytoplasm extends for a short distance only.

Birefringence gives rise to a similar question to that of variation in the argyrophil staining of the fibres of developing dentine. Collagen is birefringent but reticulin and argyrophil fibres are not.

Projecting processes when soft tissues are pulled from dentine.

In support of the view that dentinal processes occupy the tubules much importance is attached to the evidence used by Tomes (1856): "In order to demonstrate the connection of the fibrils with the pulp", he introduces a figure where the soft tissues torn from the dentine were seen as fragments projecting from its surface. He recognized the tubules and their contents as continuous with the pulp tissues that later were regarded by other authorities as being processes of the odontoblasts. A figure in his original paper is of sufficient importance to be reproduced here (Pl. 5, fig. 4). In this figure, a drawing by de Morgan, the torn tissues show channels and their walls directly continuous with the matrix bounding the tubules. No content of the tubule is evident nor are the odontoblasts shown, as is the case with illustrations of this nature by other authorities. Meyer Churchill (1935) gives an excellent account of the views at present held upon human material and in his fig. 95, "fibrils of the ground substance seen in the dentinogenetic zone," pass to the dentine matrix where tubules are shown and his fig. 97 "odontoblasts torn from the dentine" show collagen fibres projecting, although described as dentinal fibrils (compare Pl. 10, fig. 1).

A decalcified section from a two day old Tiger (Pl. 5, fig. 5) closely resembles Tomes' figure and shows the tubules empty and projecting collagen fibres from the dentine matrix in the predentine zone where the pulp tissues have been pulled away. A most convincing section of a similar nature showing all the tissues considered is from a one day old Muñtjac (Pl. 3, fig. 8). This shows the pulp tissues displaced and the collagen fibres from the matrix passing to and at the side of the odontoblasts.

A human tooth in which the pulp tissues are pulled from the dentine leaving collagen fibres continuous with those of the dentine matrix is seen in Pl. 5, fig. 9. From the same series of sections of a tooth (Pl. 6, figs. 1, 2), that had been in 10 per cent nitric acid for a fortnight, little more than swollen collagen fibres are present. The fibres although running in varying directions are mainly paralled with the long axis of the tubules.

A contrast, where displacement has not occurred, is seen in a section of a tooth from an adult Cat (Pl. 5, figs. 7, 8) the individual fibres of the matrix show their continuity with the fibres of the pulp. Some of these bundles might be regarded as passing into the tubules, but their fibrous nature is evident, and they can be traced to the more compact fibres of the matrix forming the wall of a tubule. The cells and the predentine matrix are seen to be continuous in sections from a Cod (Pl. 8, fig. 3, 4) and the more highly magnified tissues of the Grey Gurnard (Pl. 5, figs. 1, 2). This continuity of the collagen fibres from the odontoblasts with those of the matrix can also be seen in other sections, Brazilian Otter (Pl. 7, fig. 6), Bat (Pl. 9, fig. 7) and Bullfrog (Pl. 7, fig. 1). It will be seen that the collagen fibres are laterally related to the odontoblasts and appear to come directly from the cells when lying above or below them.

The organic composition of dentine and the presence of cytoplasmic processes.

Estimation of the organic content of human dentine shows that the amount present in the tubules compared with that in the matrix is insufficient to account for the presence of cytoplasmic processes. The ratio of the volume of matrix to that of the tapering tubules cannot be precisely determined. Bevelander in Orban's "Histology" (1944, p. 103) says of human dentine "The ratio of the number of tubules per unit area on the pulpal and outer surface is about 4 to 1"; he quotes Lehner & Plank (1937): "Near the pulpal surface of the dentine the number of tubules in one square millimetre varies according to some investigators from 30,000 to 75,000". It is obvious in any section of dentine that the tubules bear an appreciable ratio to the matrix as in the tooth of a Shrew (Pl. 3, fig. 9).

Charles Tomes estimated the organic matter in dentine as 19.6 per cent which approximately agrees with the most recent estimate. Stack (1951) who determined the organic constituents of human dentine by estimating the amount of nitrogen present, found that "'average' dentine contains 20 per cent organic matter". He concludes:

"It can now be stated that 'average' dried dentine contains 18 per cent collagen, 0.9 per cent citric acid and 0.2 per cent each of insoluble protein, mucopolysaccharide and fat; the inorganic constituents (excluding water) total 75 per cent."

Leicester (1949) states:

"Rosebury (1930) noted that when dentine was extracted with water, the extract gave a positive biuret test, indicating the presence of some soluble protein. This work was extended by Karshan, Weiner & Stofsky (1934), who showed that in three successive aqueous extracts of crushed dentine, 0.3, 0.065 and 0.02 per cent protein were dissolved. This protein was assumed to be present in the fluid of the dentinal tubules. Thus, in spite of the small amount of recent work on the dentine protein, there seems no reason to doubt its essentially collagen nature although a small amount may be present in soluble form."

Stack (1951, p. 179) says :

“ All the protein of the organic matrix appeared to be collagen and any histological evidence to the contrary may be explained by the very small amount of protein detected . . . ”

and he also says referring to skin and dentine collagens (p. 180) :

“ Examination of the amino acids ‘ spectra ’ reveals very slight differences but it was noted that bone and dentine collagen resembled each other more closely. ”

Many interpretations of the nature of the contents of the dentinal tubules are expressed, but if cytoplasmic processes from the odontoblasts are present throughout their extent an appreciable amount of protein should be present.

PREVIOUS OPINIONS UPON THE CONTENTS OF THE DENTINAL TUBULES

Contents of the dentinal tubules have been extensively discussed in the literature. Cytoplasmic processes from the odontoblasts are constantly assumed to be present and questioned only by Mummery and Klein (see page 15).

Prepared specimens and numerous illustrations of histological sections, chiefly of human or laboratory animal material, show coagulable contents in the tubules commonly called “ dentinal fibrils ”. Their presence is regarded as providing the chief evidence supporting the opinion that processes from the odontoblasts are present. Many views are expressed about their exact nature and several claim, like Hopewell-Smith (1903) quoted on page 15, that cytoplasmic processes extend into the finest ramifications of the tubules.

Some of the illustrations of sections in the literature claiming to show fibrils in the dentinal tubules are due to an optical effect at different focal levels. When the tubules are cut transversely a ring with no apparent content may be seen but a slight change of focus gives a central dark spot occupying the former clear ring (Pl. 6, fig. 1, 2). This dark spot has been regarded as a dentinal fibril cut across. Longitudinally cut tubules also vary with the depth of focus, clear tubules can be made to show a “ fibril ” when the border of the channel is so focused ; or may be seen as a crescent if the tubule is cut obliquely, Rat (Pl. 6, figs. 3, 4). In a section from the tooth of a Chimpanzee (Pl. 5, fig. 3) similar appearances are seen. Where several tubules are parallel, if the section is moved across the field the change from clear channels to dark lines resembles the small ripples on the surface of water.

The contents of the tubules in a fluid or a sol state are most commonly not stained, giving rise to the empty appearance, possibly there is some loss in preparation of the more fluid content. Coagulated colloidal particles near to the pulp may be stained where the tubules are wider and larger. Fragmented particles are described as broken “ fibres of Tomes ” by Bradford (1950). The fragments seen in transverse sections of the tubules of the Three-toed Sloth that were completely cut off from the odontoblasts (Pl. 6, figs. 6, 7, 8) support the contention that they are coagulated substances of tissue fluid. The contents of the tubules in the Two-toed Sloth also cut off from the odontoblasts are shown in a highly magnified section (Pl. 6, fig. 5). Such a section is difficult to interpret for a tubule cut obliquely shows a dark cone indicating an optical effect.

Kramer & McLean (1952) demonstrated coagulable material in the tubules of human dentine attributed to aspiration of odontoblasts, a more likely explanation

is that the coagulable fluid is a reaction to irritation, whatsoever the explanation the presence of fluid of this nature is of interest.

Expressions upon the nature and arrangement of the contents of the dentinal tubules are conflicting. Many recent opinions favour complete occupation by the fibril. John Tomes (1856) was not sure whether the fibrils were tubular or solid as already quoted (p. 14). Other observers have suggested that the cell processes from the odontoblasts are hollow. Bodecker (1953) states, " the dentinal fibrils do not appear solid but as hollow tubes " and he quotes authorities using the electron microscope :

" Recently Scott, Albright, Sognnaes and Wyckoff (1952) have clinched the concept that the dentinal fibril is tubular in character. . . . ' Of course, we have no evidence yet as to what may have been inside, or possibly around, such fibres but I think you will be quite safe in assuming that the fibre is thin-walled and of a generally tube-like character.' Thus contrary to the accepted idea, dentine appears to be traversed by a system of delicate tubes instead of solid fibres radiating from the pulp."

Further investigations with the electron microscope upon a human premolar by Schroff and others (1954) state that :

" The dentinal tubule, as presently accepted from examination of decalcified sections, is not the true picture of the structure existing during life. It is a canal with walls composed of highly inorganic material, much harder than the surrounding matrix and enclosing in its centre the odontoblastic process. The diameter of the actual canals, therefore, is only that of odontoblastic process, approximately 1 to 1.5 μ . There is no appreciable space for the diffusion of tissue fluid around this process."

Orban (1944, fig. 77, p. 107) is of particular interest, for the empty appearance of the dentinal tubule is explained as " well fixed decalcified section of dentine " and " no shrinkage between dentinal fibres and dentinal tubules".

An extensive analysis of the many views expressed is made by Hanazawa (1917). He points out that the tubules were recognised by Leeuwenhoek (1722) and traces the different opinions of observers up to the time of his own conclusions. The nature of the dentinal fibril is regarded differently by authorities, as cytoplasmic, tubular with fluid content, solid or fragmented, previous authorities are also uncertain whether the tubule is completely occupied or space exists between the fibril and the containing wall, and whether a sheath exists which is the cell membrane or a new formation. A clear area around the fibril is also discussed, as are also the fine branches from the tubule and fibril.

Hanazawa discusses the solid and tubular appearances in transverse sections and comments upon the different appearances due to variations of focus upon a section. Marett Tims in the Eighth Edition of Tomes' Dental Anatomy (1923, p. 81 *et seq*) very fully considers the presence of dentinal fibrils in the dentinal tubules and their relation to the odontoblasts.

Meyer-Churchill (1935, p. 49), a widely accepted authority, says :

" Within the dentinal tubuli we find extension of the odontoblasts or peripheral pulp cells which produce the dentine, or, at least, play an important part in the genesis of this structure. This extension of the odontoblasts, which after its discoverer is also known as Tomes' fibril, lies *in vivo*, almost in direct apposition to the wall of the tubule. *Only traces of tissue fluid circulate for metabolic processes between the fibril and the tubular wall.* (The italics are mine).

Bradford (1950), in a study of Tomes' fibres in human dentine, says it is "a soft cytoplasmic core which is the dentinal process of the odontoblast cell, and an outer sheath of mucoid tissue" and concludes: "The protoplasmic core of Tomes' fibre is very fragile and fractures soon after extraction of the tooth", his fig. 6 shows "the fractioning of the core of Tomes' fibre".

MacGregor (1936, p. 1237) injected lead acetate, later converted to the sulphide, to demonstrate the lymphatic system of the teeth, the dentinal tubules were penetrated as is well illustrated in his fig. 10. These extensions outside the lymphatic system, which is a closed system, must be through a ruptured endothelial wall into the tissue fluid cone. This penetration into the dentinal tubules could hardly occur if they are occupied completely by cytoplasmic processes.

The presence of a lining to a dentinal tubule known as the sheath of Neumann is much discussed by observers and several attribute it to the cell wall of the process of an odontoblast.

Sharp definition of the walls of the dentinal tubules is not evident in decalcified sections nor is it more obvious in the ground sections as seen in human dentine (Pl. 9, fig. 4). An impressive feature is that the individual bundles of collagen fibres of the matrix are distinct in this *ground* section. A difference in detail of structure between the tubules and matrix of mammalian dentine appears to be more complete than in the channels or spaces and matrix in other vertebrates. These features are seen in the Muntjac and Shrew (Pl. 3, figs. 8, 9), *Amia* (Pl. 7, fig. 7), *Iguana* (Pl. 8, fig. 5), *Lepidosiren* and *Protopterus* (Pl. 9, figs. 1, 6) and others. Ground sections are rarely satisfactory for definition of detail as they are usually too thick. Bradford (1951) who restricted his observations to the surface of the section which alone was focused, the section having been reground after staining, describes a translucent area around the fibril that was stained with a reduced silver technique. It would seem that the cementing substance of the matrix in this position is devoid of collagen fibres. This appearance is discussed by Kramer (1951), he quotes Lefkowitz (1943) "That the peritubular collagen-free zone is deposited after the rest of the dentine matrix has been formed." Kramer in his conclusion says: "Except in the dentine nearest the pulp, each tubule is surrounded by a collagen-free zone." The thinner layer of cementing substance with the collagen fibres nearer the margin of the orifice of the tubule is of interest as these fibres are evident when the pulp tissues are pulled away as seen in Tomes' figure reproduced here (Pl. 5, fig. 4), the Tiger (Pl. 5, fig. 5) and other figures. The last formed fibres of the matrix lining the tubules appear to be more compact, some elastin was suggested by C. Tomes (1895-6) who is quoted by Stack (Randall *et al.*, 1953, p. 128). Many authors deny that the sheath of Neumann has a special structure, but in a recent statement by Maximov & Bloom (1952, p. 348) we find:

"The layer of dentine which is immediately adjacent to the tubules and surrounds them as a sheath of Neumann differs from the rest of the dentine by its high refringence and distinct staining in decalcified specimens."

Mummery (1924) quotes Hoffe (1862) stating the sheath is present in fossil material. A difference in concentration of collagen fibres may account for the appearance of a sheath.

That the connection of "dentinal fibrils" with the odontoblasts is not clearly demonstrated is remarkable when so constantly stated, and also assumed from demonstration of the presence of contents seen in histological sections.

The writer concludes that tissue fluid occupies the tubules or spaces permeating dentine matrix and that dentine is similar in nature to other connective tissues.

Nerve fibres are regarded by authorities as being present in the dentinal tubules but have been demonstrated for only a short distance. They need to be mentioned as a possible content.

THE NATURE OF TOOTH DENTINE

Having discussed some important aspects of tooth-dentine, reviewed the opinions expressed by authorities upon the nature of the contents of the dentinal tubules and presented evidence to show that cytoplasmic processes from the odontoblasts are not present in the dentinal tubules, we now need to consider certain other features of the nature of tooth-dentine.

Dentine with a matrix of ground substance permeated by tissue fluid is in structure similar to the less as well as the more condensed forms of connective tissue. Odontoblasts like fibroblasts, in being fibrogenetic are responsible for the production of the collagen fibres and cementing substance of the dentine matrix. The tissue fluid, supplying nutriment to the odontoblasts and occupying the dentinal tubules, has been very little studied.

The advance in knowledge of the ground substance of the connective tissues has an important influence upon our understanding of the nature of the dentine matrix. The general conclusions reached are significant, as they coincide with the writer's conception of continuity of structures produced by the odontoblasts with the dentine matrix, and *not* as processes in the dentinal tubules.

The extensive studies of the components of the ground substances of the connective tissues, in particular of collagen and mucopolysaccharides, are recorded in many papers, in collections by Randall (1953) and Asboe-Hansen (1954) and in recent communications to "Nature" (1955-56).

Robb-Smith (1954) says :

"Connective tissue can be defined as tissue fluid in a matrix of mucopolysaccharides and scleroproteins, in varying degrees of polymerization but largely disorientated, in which are lying orientated fibres of varying thickness of collagen and elastica."

This statement is made of the ground substance, and although making no reference to the cells, is of interest in that a distinction is drawn between tissue fluid and matrix. These observations upon the nature of connective tissues if applied to dentine are better understood when it is considered as a developing tissue rather than as an almost static formed structure.

Odontoblasts have long been recognized as responsible for the formation of dentine. Mummery (1892) determined the presence of fibres in the matrix and von Korff (1905, 1930) described the arrangement of fibres during dentine development. Tomes, as previously mentioned, quotes Lent and Kölliker with the statement that processes from the odontoblasts are present in the tubules

and that the matrix is formed around them, the opinion commonly held. Meyer-Churchill (1935, p. 215) says of odontoblasts: "During odontogenesis their cytoplasm forms extensions which occupy the dentinal tubuli". The tubules were regarded as being maintained by the persistence of the dentinal fibrils.

These interpretations are no longer tenable and the writer concludes the tension of the tissue fluid is the factor determining the arrangement of the components of the dentine matrix during development, including the form of the "tubules" which should be regarded as connective tissue spaces.

The production of collagen fibres and cementing substance of tooth-dentine.

The intracellular or extracellular production of collagen fibres from fibrogenetic cells although much discussed, is not of great significance in dentine development for the ultimate formation is extracellular. That the primary stage of formation is intracellular may be possible, as seen from the appearance of granules and possibly fine fibres in the cells and their extensions into the predentine matrix. Mallory (1903) described intracellular fibres in connective tissue cells and called them fibroglia, as did Porter (1951). S. Fitton Jackson (1954-55) described intracellular granules and fine fibres in osteoblasts and other fibrogenetic cells; this applies to odontoblasts where the appearance of granules closely resembles those seen in the osteoblasts (Pl. 4, figs. 5, 6, 7, 8, 9, Pl. 5, figs. 1, 2). The presence of a polysaccharide is recognized as the cementing substance of dentine, which with the collagen fibres depends upon the odontoblasts for its development. Jackson says of granules in fibrogenetic cells in tissue culture: "So far as can be ascertained, both protein and polysaccharide are present in the same granule". She demonstrated at a meeting (July 1954) of the Anatomical Society at Cambridge, granules in osteoblasts which have an appearance closely resembling those seen in odontoblasts. The distinction between active cytoplasm and its products is not easily drawn.

The dentine matrix.

The collagen fibres of the formed dentine matrix can be demonstrated in decalcified sections (Pl. 3, fig. 8, Pl. 4, fig. 3, Pl. 5, figs. 5, 7, 8) and also in ground sections not decalcified (Pl. 9, fig. 4), (Pl. 3, figs. 1, 2, 3).

Unfortunately, decalcified sections are of little value for demonstrating the cementing substance and ground sections which are necessarily thick with a calcified matrix, reveal too little of the detailed structure. In the ground section of human dentine (Pl. 9, fig. 4) thin enough to allow the unusual use of an oil immersion objective, the cementing substance is not evident, nor is there sharp definition of the walls of the tubules, but the fibres in the matrix are apparent. Preparation of specimens, and staining methods, need to be more fully explored with the possibility of demonstrating the cementing substance.

The remarkably uniform appearance of the dentine matrix seen in sections cut either longitudinal or transverse to the tubules, gives no evidence of localized production by individual odontoblasts as might be expected. Their products must blend and form the homogeneous matrix which caused Mummery (1892) to undertake his investigations.

The writer is of the opinion that the tissue fluid pressure determines the arrangement of the components of the dentine, which blend as they are produced by the odontoblasts to form a uniform matrix. The laterally contained tissue fluid gives rise to the cylindrical or tubular form of the channels.

Calcification although not discussed here affects histological appearance during development, Ham (1953) explains the presence of a predentine layer as due to insufficient phosphatase when compared with bone development, where calcification occurs immediately the preosseous matrix is laid down. This delay, if correctly interpreted, would lead one to think that calcification depends chiefly upon the tissue fluid, for the odontoblasts are not then directly associated with the area in which calcification is taking place, as it occurs successively against the formed dentine in the predentine farthest away from the odontoblast layer of cells. The phosphatase although widely produced may still be supplied by the odontoblasts.

HISTOLOGICAL APPEARANCES IN DENTINE DEVELOPMENT

The production of dentine can be studied histologically at successional stages.

Initiation.

Evidence of cells that will differentiate into odontoblasts and other pulp cells is well shown in a section through the terminal aspect of a dental lamina in *Rana catesbiana* (Pl. 7, fig. 2). Differentiation and proliferation of mesenchyme cells (commencement of the shower described later) is seen opposite to the localized group of differentiated columnar cells, noticeable by their elongation in the dental lamina upon the "face adamantine" of Pouchet & Chabry (1884). Later these special cells form the internal dental epithelial layer lining the cup of the bell-shaped enamel organ enclosing the related mesenchyme cells which proliferate freely.

A noticeable collection of differentiated mesenchyme cells is always seen in association with the dental epithelium in its early development. The mass of these cells with deeply stained nuclei emphasizes the position of the rapidly growing enamel organ (Pl. 7, fig. 4) and later many cells are densely set in the pulp area. These mesenchyme cells are so noticeable and constant at all stages in their relation to the developing dental epithelium that I have named them "the shower".

Tonge (1951 & 1953) discusses the distribution and arrangement in human embryos of the condensations of the mesenchyme cells that are related to the development of the teeth and bones of the jaws.

Development of the odontoblasts.

The differentiated cells giving the shower appearance have no particular individual form until the enamel organ assumes the cap or bell shape, when cells at the surface of the pulp area undergo further differentiation into characteristic odontoblasts, being larger and more elongated than the other mesenchyme cells. The first indication is preceded by a change in the cells of the internal dental epithelium of the enamel organ, where those at the centre over the summit of the

pulp area elongate and become more sharply defined. These cells act upon the mesenchyme cells, an influence attributed to organizers, and induce the changes giving rise to the special odontoblasts at the surface of the pulp. The odontoblasts are spaced in a varying degree and are vertically orientated to the basement membrane, the arrangement can be seen in most sections from mammals and is well shown in reptiles in Pl. 4, figs. 7, 8 where some dentine is formed. They have a definite relationship to structure and to the tissue fluid channels, which are more regular in mammals, both during and after development of the dentine, than in other classes. Although the odontoblasts are spaced, they are sufficiently close to have a palisade-like appearance, an arrangement suggesting that lateral pressure determines the shape of the cells. The arrangement of these cells without close contact is in marked contrast with the tight palisade-like relation of the cells of the internal dental epithelium. These epithelial cells are so compact as a layer, that displacement from one another in prepared sections is rarely seen; Pl. 4, fig. 2 shows a layer broken without cell displacement. Even where most marked disarrangement of other tissues occurs it is noticeable. This firm arrangement is represented diagrammatically in Text-fig. 4, page 32.

Marginal extension of the odontoblasts.

Full differentiation of the odontoblasts occurs in sequence, following changes in the cells of the internal dental epithelium, commencing at the summit of the pulp, where a dome or cap of odontoblasts is seen which extends progressively at its rim. Addition of cells occurs as far as tubular dentine formation occurs; in the contracted type of root it continues to the end of the tooth, in a tooth with an open base it continues until the bone of attachment connecting it to the supporting bone is produced. The extent of the tubular dentine is shown by an invariably constant feature, the "fold" formed by the junction of the internal dental epithelium and external dental epithelium at the lower margin of the enamel organ. This applies to tubular tooth-dentine in all vertebrates, and in the opinion of the writer always precedes the formation of any other recognized form of dentine, such as osteo-dentine or the trabecular dentine of elasmobranchs.

Tubular dentine progressively develops by addition at the advancing margin and increases in thickness by deposit upon the pulp surface of the formed dentine. As dentine is produced, the internal dental epithelial cells become reduced in a regular sequence, inversely corresponding with the increasing development of the odontoblasts. The flattening of these epithelial cells is well seen in the development of the placoid scales of the elasmobranchs.

The function of the tooth pulp.

The only function of the tooth pulp, the formation and maintenance of dentine, needs to be emphasized, for the odontoblasts are the essential cells, the arrangement of the pulp tissues being directed solely towards their function and nutrition. Most significant is the arrangement of the odontoblasts and their blood supply beyond which dentine is formed and situated James (1955), see also page 30 and

Pl. 7, fig. 5, Pl. 8, figs. 1-8. A marked contrast is to be seen when a comparison is made between this formation of dentine and of bone with included cells and blood capillaries.

Cells of the "shower" beneath the enamel organ become the formed pulp with odontoblasts at the surface. This pulp area is invaded by vessels and nerves, but the exact sequence in development of the different structural elements becoming the completed pulp, is not known in detail. The development of nerve fibres in the persistently growing incisor of the rat has been described by Powers (1952).

Basement membrane and related fibres.

A basement membrane between the internal dental epithelial cells and odontoblasts can, with special staining, be demonstrated as a reticular network at the surface of the pulp. This reticular structure is chiefly mesenchymal, but is in some degree mixed with fine fibres from the cells of the internal dental epithelium. In *Scyliorhinus canicula* (Pl. 10, fig. 8) on the right side of the figure the basement membrane is cut transversely and seen as a line with the cells on each side approximately vertical to it, the slightly oblique deviation in cutting accounts for the wide line appearance of the basement membrane. At the upper part of the section the greater obliquity of the plane of cutting shows fibres interlacing and irregularly arranged.

According to Bevelander (Orban, 1944, p. 119) thickening of the basement membrane is the first sign of dentine development.

The formation of the collagen fibres of the dentine matrix occurs in relation to the reticular fibres of the basement membrane and those passing from it. The phases of development through which the fibres pass are expressed in their response to silver stains, the reticulin and argyrophil fibres stain deeply and are distinct from the reaction of formed collagen fibres which are not argyrophil. The reticulin fibres branch and anastomose as a very fine reticulum but their relation to the non-branching collagen fibres is not clear. The argyrophil fibres are usually regarded as precollagenous but it may well be collagen fibres are built upon pre-formed reticular fibres. The statement by Glynn (Randall, 1953, p.46) is of interest:

"Almost all the evidence which is available seems to fit in with the hypothesis that reticular fibres are essentially collagen fibres, but that there is a more intimate relation to polysaccharide to which the whole complex owes its argyrophilia, and this is lost when the polysaccharide is previously removed."

Fibres in the early granular stages of development are not demonstrated, possibly through being lost in preparation. Fibres described by von Korff (1930) as argyrophil, quoted by Orban (1944), Meyer (1935), are said to originate deep in the pulp and merge with the fibrils of the basement membrane. Von Korff's figures show the bundles of fibres from the basement membrane passing the sides of the odontoblasts and separating into fine fibrils in the pulp. Bevelander (1941) in a study of the arrangement of the collagenous fibres comments upon sections of teeth from 130-160 mm. pig and seven and a half months human foetus. His conclusions with regard to the formation of the reticular fibres are given in detail for they

do not agree with those stated in this paper as occurring with development of the tissues and not by an invasion as is implied.

"It is interesting to note that the odontoblasts can first be recognised as columnar cells in the region in which the first radial fibres appear. In the most coronal part of the tooth certain other changes are apparent. In the first place, the radially disposed reticular fibres, i.e. Korff's fibres, now arise fairly deep in the pulp tissue considerably below the odontoblasts. They pursue a direction which is sometimes straight, sometimes tortuous, acquiring more fibrils meanwhile until they reach the distal surface of the odontoblasts. Just beyond this zone, they splay out into a number of extremely delicate fibrils which run approximately parallel to the dentinal tubules. The terminal portions of these fibrils which can be observed at the dentino-enamel junction are more intensely argyrophilic than is the case in other parts of the developing dentine."

The production of predentine.

Although based largely upon sections of mammalian tissues the following details can be given a wide application, for the relation of the odontoblasts to the forming dentine matrix is remarkably similar in all vertebrates. The earliest stage in the formation of predentine is at the summit of the pulp, where the odontoblasts are against the basement membrane, and the forming predentine layer is composed of granules and fine fibres with the commencement of tissue fluid channels.

The section (Pl. 4, fig. 10) from a foetal kitten (9.8 cm.) shows this very early stage where fine granules take the form seen later in predentine. The tubules, just evident, are best seen by following the intercellular spaces from the pulp. An odontoblast shows a conical cytoplasmic end, the others are more rounded, all have tiny granules and a suggestion of fine fibres connected with the basement membrane.

The granules and fibres are more evident when silver stained but the cells are hardly seen, the fibres are seen in Pl. 10, fig. 2; in Pl. 10, fig. 4, a more highly magnified section from a foetal lamb of eighty-nine days and Mallory stained, different phases of development can be seen. The cells, best seen with a lens, show stages of fibre formation. Fibres vertical to the basement membrane are evident on the right side, some as darker and closer bundles in the centre, whilst on the left, dentine production is just beginning. The nuclei are deeply stained and the fibres forming the matrix are related to the cells.

The difference in the staining of the argyrophil fibrils and collagen fibres accounts for the different appearances seen in sections. If the thicker collagen fibres do not stain, their relation to other structures cannot be determined by silver stained sections. A section of a tooth from a Cod (Pl. 10, fig. 6) shows argyrophil fibres deeply stained in the region of development, but the difference between mammalian and piscine tissues may be appreciable with varying staining reactions.

Predentine.

As development progresses a definite layer of predentine is clearly distinguished from the formed dentine in microscopical sections. This distinction, seen through staining, depends largely upon whether the tissues were previously calcified or not, but there may be additional factors for the appearance is sharply contrasted. The

distinction is discussed by Greulich & Leblond (1954) using tracer elements. Radio-autographic recording of radio-elements in newborn and three days old rats showed the elements to be present at intervals at the ends of the odontoblasts, then in the predentine and later in the dentine. The site of deposition was demonstrated in the predentine, and seen later in the formed dentine, moving farther and farther from the odontoblasts. The presence of the elements in the formed dentine, although becoming less defined with progressive development, shows a stability not experienced in most other tissues. The low metabolic interchange of formed dentine accounts for their presence.

A decalcified section from a two day old Tiger (Pl. 5, fig. 5) is of interest, for remains are seen of the collagen fibres, the pulp tissues having been pulled away. A characteristic appearance of the odontoblasts and the predentine is presented in sections from a lamb (Pl. 3, fig. 10, Pl. 4, fig. 5); the long narrow cells with granular cytoplasm and nuclei at the pulp end are directly connected with the dentine matrix. There is the usual empty appearance of the dentinal tubules passing to the spaces between the odontoblasts. The granular nature of the cells and of the matrix of the predentine is well shown in sections, highly magnified, in the American Copper-head Viper (Pl. 4, fig. 7), the Australian Tiger Snake (Pl. 4, fig. 8) and also in the lamb (Pl. 4, fig. 5).

The predentine matrix is composed chiefly of granules which are directly continuous with granules in the cytoplasm of the odontoblasts. The relation of the granules to the cell wall, present at the sides and at the pulp end of the cell, is not defined towards the predentine. In the sections (Pl. 3, fig. 10, Pl. 4, figs. 5-9, Pl. 5, figs. 1, 2) the cell membrane is absent as a definite structure at the distal end of the odontoblasts. The distinction as to where the cell ends and the matrix begins is so ill-defined that it cannot be determined. The cell granules are generally large, becoming finer in the matrix of the predentine, although, in the coloured photographs the reverse of the very fine granules is suggested (Pl. 2, fig. 2). They tend towards a linear arrangement in the long axis of the cell and the tissue fluid channels between them are continuous with the dentinal tubules (Pl. 3, fig. 10, Pl. 4, fig. 5). Granules form in the odontoblasts in a manner similar to other fibrogenetic cells, with which the developing fibres may be so closely related as to appear to come directly from the cell particularly those lying above or below it.

A misinterpretation of this relationship of the fibres to the cell accounts for the error of regarding odontoblasts as having cytoplasmic processes in the dentinal tubules. The matrix is built up by addition to the surface forming the wall of a tubule as well as the extension of the continuity between the end of the cell and the matrix. Fibres that appear to enter a tubule will if followed, be seen to join the wall of the tubule. The appearance can be deceptive, but bundles of fibres are always seen to join the matrix with the usual empty appearance of the tubule beyond (Pl. 3, figs. 4, 8, Pl. 4, figs. 3, 4, Pl. 7, fig. 3 and others). The coloured illustrations (Pl. 2, figs. 1, 2, 3) demonstrate the cytoplasmic cones and the collagen fibres passing to the matrix which with selective stains are red, while the granules lying between them also passing to the matrix are stained green or blue.

The initiation of production of the collagen fibres in dentine development is difficult to establish. At an early stage their formation, as already mentioned, appears to be at the end of the cell, yet in the more developed stages it occurs at the sides (Pl. 10, figs. 2, 6), coinciding with the work of Mummery (1892) and von Korff (1905, 1930). The ends of the matrix towards the predentine are narrow and rounded and the completion of the tubule at the pulp end is seen with fibres passing to its wall (Pl. 5, fig. 6 and others). Fine collagen fibres according to Martin (1953) are destroyed by acid, and although rarely seen in early predentine, they must be forming, as suggested in the kitten section Pl. 4, fig. 10 (Schiff stain). That the early formed fibres are not firm is evident from the all too frequent displacement of the odontoblasts from the predentine as seen in prepared sections (Pl. 2, figs. 1, 2) where fibres have formed and the tissues are held.

DENTINE AND TISSUE FLUID

Dentine as in all tissues has two essential components, one relatively fixed and characteristic in structure, the other a pervading tissue fluid, the distribution and composition of which varies according to the metabolic demands of the related cells needed for their survival and for the structures produced by them. Nutrition of cells, conveyed through the tissue fluids, is the key to the understanding of all tissues.

Descriptions of tooth-dentine are in the main based upon what is known of the matrix, for although the presence of tissue fluid is recognized, it is seldom considered. When the contents of the tubules are examined, attention is directed almost entirely to interpreting the assumed presence of cytoplasmic processes from the odontoblasts. A structural feature without any explanation of why they are there, it is true the possibility of transmitting sensation is suggested, and the development of the matrix was thought to depend upon them.

The marked contrast between the active stage of development and the passive state of formed dentine is recognized in the arrangement of the odontoblasts and their blood supply.

The Vaso-cellular barrier.

The nearness of the blood capillaries to the odontoblasts during development allows nutriment to be conveyed almost directly to the cells producing dentine. In this the odontoblasts are akin to osteogenetic cells in bone which have an intimate relationship with the blood capillaries. Although the measurements between odontoblasts and capillaries have not been made the conditions are closely similar. Ham (1952 & 1953) who made measurements from the bones of dogs and found that an osteocyte is never more than 0.50 mm., and far more frequently 0.10 mm. from a blood vessel, says: "... the canalicular mechanism cannot operate effectively over greater distances...."

The intimate association of the capillaries and the odontoblasts has been demonstrated in a wide range of vertebrates, James (1955). The relationship is best seen in injected specimens, as in the Hamster and kitten (Pl. 8, figs. 7, 8). When not injected the capillaries are recognized by the presence of erythrocytes and by

the presence of the nuclei of the endothelial cells of the vessel walls. (Pl. 8, figs. 1, to 8, and others).

This layer of odontoblasts and capillaries needs a distinctive name and the writer suggests "Vasocellular-barrier". The term "barrier" is used for the blood vessels to the central nervous system.

In teeth, with either an open base or contracted root, the position and relation of the tissues and vessels do not differ greatly. The capillaries carrying nucleated erythrocytes are larger, but they are always in close relation to the odontoblasts (Pl. 8, figs. 4, 5, 6) although rarely among them. In mammals with non-nucleated erythrocytes the smaller capillaries are finer and in closer relation with the cells (Pl. 8, figs. 7, 8) coinciding with an increase of metabolic demands, Baldwin (1949). Obviously the pabulum is necessary to the cells and not to the forming dentine.

In formed dentine the nutritional demands are much reduced. The finest tubules and canaliculi can contain little more than a solution of salts and water. Formed dentine has neither cells nor blood vessels, and as production of dentine progresses that formed first becomes gradually more distantly placed from the Vaso-cellular barrier thus accounting for its characteristic acellular and avascular structure.

The conception of dentine consisting of tissue fluid permeating the matrix without the presence of cytoplasmic processes, and the view that the dentine matrix is not formed around these processes, will be revolutionary to many, for this conclusion is contrary to the usual interpretation of bone development, which has undoubtedly influenced previous conceptions of dentine production and structure.

Bone development and structure are beyond the scope of this paper but, the syncytial connections between bone cells has undergone criticism, Ham (1953) says :

" osteoblasts are provided with cytoplasmic processes which act as moulds when the organic intercellular substance is laid down around them, and hence, when the cytoplasmic processes subsequently retract or shrink, tiny canals (canaliculi) are left in the intercellular substance." And he remarks (fig. 126d. legend) " when calcification occurs canaliculi remain to conduct tissue fluid to osteocytes."

The withdrawal of cytoplasmic processes from the dentinal tubules has not been suggested, nor is there any histological evidence in support of such an explanation. The question may be raised whether the presence of cytoplasmic processes, and especially as a syncytium, is true for the development of bone ? The development of dentine in the writer's opinion, depends upon the formation of the matrix by odontoblasts around intervening channels conveying tissue fluid under sufficient pressure to maintain them.

VARIATION OF PRESSURE AND TENSION IN THE TISSUE FLUIDS UPON TOOTH DEVELOPMENT

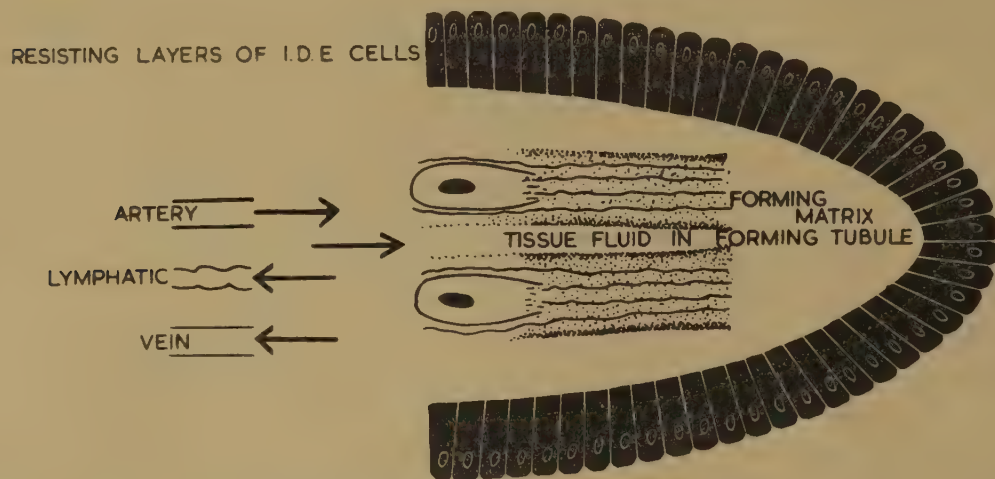
The volume of the tissue fluid and the growth of cells establish a momentum that exercises a recognizable pressure and tension upon the arrangement of the tissues during development of the teeth and upon tooth eruption. To determine the effects of these forces further investigation is needed, but the structural detail of

the dentine matrix with interspaces radiating from the pulp surface indicates a centrifugal force, acting upon the developing tissues. This force is controlled externally by the layer of the internal dental epithelial cells of the enamel organ commonly in the form of a cone. (Text-fig. 4.)

That variation of tension occurs in the intercellular tissue fluid and ground substance of connective tissues has been known since the work of Starling (1895-6, 1909).

Graded vascular blood pressure is at a minimum in the finest capillaries, where the filtrate becomes the tissue fluid with a pressure sufficient to convey nutriment to the cells, a balance being maintained by variations of diffusion and osmotic pressures. Regional variations in the composition of the tissue fluid are the result of osmotic activity associated with products of the local cells, for there is no evidence, beyond changes of pressures, that endothelial cells of the capillaries are selective.

Fig. 4.



The rigid cone of the internal dental epithelium (IDE) which controls the pressure and tension of the tissue fluid determining the arrangement of the developing dentine structure. The variation of fluid pressure between the filtrate from the blood capillaries to the return by the veins or lymphatics is a definite feature however complex. The cone becomes occupied by dentine, composed of a matrix and tubules containing tissue-fluid enclosing the pulp. A mammalian tooth is represented being more easily demonstrated.

Tissue fluid is no longer regarded as a watery solution with suspended substances but as having a viscid consistency holding particles so that free movement does not occur, as shown by Bensley (1934).

Drinker (1941, p. 44) discusses the changed conception of tissue fluid and says :

" In addition to the colloid osmotic pressure, the filtration of fluid from the capillaries is resisted by what is called tissue pressure. Under normal circumstances, the space for fluid outside the capillaries is slight, and if one stabs the skin with a needle, one cannot obtain clear fluid. But if edema occurs, the tissues are separated forcibly, and after a short time, puncture wounds will supply clear edema fluid containing varying amounts of protein."

In a new edition Yoffey & Courtice (1956, p. 64 *et seq*) the " Starling hypothesis ", " Factors concerned in filtration " and " Tissue pressure " are discussed.

Whatever views are held, nutriment passes from the blood stream through the intercellular tissue fluid to the cells. The degree of fluidity of the tissue fluid varies from a complex colloid to a composition of little more than water and salts.

Sherrington (1951) comments that although the study of the tissues is made in great detail little reference is made to the body being composed chiefly of water. The most recent estimate of "total body water", Pawan (1954) gives the normal as being 50 to 65 per cent, a variation occurring with age and obesity. The lymph derived from the tissue fluids returning to the blood stream is fluid and similar in composition to the blood serum.

Ham (1953) states that tissue fluid exists as a free fluid, as the dispersion medium of a sol or of a gel, or in various combinations.

The influence of variation in pressure and tension as constant factors upon the arrangement of forming elements, and the relations of the cells and developing tissues to one another has been little considered, but as tissue fluid is not static and possesses momentum the influence it exerts upon the structure of dentine during development is of the greatest importance.

The intercellular fluid in all tissues must be under sufficient pressure to maintain the permeability of the tissue structures and to vary sufficiently for the metabolic interchanges of the cells. Nutriment is supplied almost directly to the odontoblasts from the blood capillaries by reason of their close relationship. The amount of fluid varies as dentine is formed, but tissue fluid spaces are histologically evident in all developing dentine. The basal layer of Weil would appear to be a wide tissue fluid space and may have significance in its close relationship to the odontoblasts (see Pl. 2, figs. 1, 2). The arrangement of the tissues is determined by the pressure upon the plastic bundles of fibres and cementing substance of the developing dentine matrix. The fluid pressure radiates from the pulp, passing intercellularly exercises stresses in the tissue fluid upon the forming matrix of dentine, establishing the tubules and canaliculi. This interpretation by the writer replaces the long accepted view that the dentinal tubules are formed around the arborescences of processes from the odontoblasts.

An increase in volume of the developing tooth cannot occur without an increase of pressure in the fluid components of the tissues. When the tubules in dentine are cylindrical it is due to fluid being laterally contained, and their curvature probably explained by d'Arcy Thompson's (1942) observation that this occurs when the length of a cylinder becomes three times as great as the diameter. If this accounts for the curvatures in dentine it must occur in a sufficient length of tubule prior to calcification and an associated width of the predentine area.

Increase in the number of cells and pressure of tissue fluid must occupy more space which can be obtained only in a superficial direction, and with this surface movement the dental epithelium (in mammals) unfolds over a tooth, in the same manner that epithelial laminae split during development, like the bucco-gingival fold of epithelium and other similar epidermal covered tissues separate. The central epithelial cells of the dental lamina may be seen to undergo keratinization as epithelial coils in the dental epithelium over developing tooth-germs

(James, 1909). As the production of epithelial cells progresses the central cells of an epithelial fold removed more and more from nutrition undergo degeneration. The tooth with structures attached becomes exposed, it does not move through the tissues for eruption as was formerly thought.

Control by the internal dental epithelium on tooth development.

Development of all teeth depends upon an enamel organ of characteristic structure, with an essential layer of internal dental epithelial cells. This is a remarkably rigid layer and is seen to remain with its cells in close contact in histological sections, even when considerable displacement of other tissues occurs. In (Pl. 4, fig. 2) enough displacement has occurred to demonstrate this. This firm layer of cells in the form of a cone resists the radiating pressure and tension present in the tissue fluids of the pulp (see Text-fig. 4, p. 32).

This unyielding internal dental epithelial layer determines the shape of the tooth, James & Wellings (1943). The structural detail in the arrangement assumed indicates the pressure and tension present. The influence of fluid pressure is seen in most sections of developing teeth as in the Python (Pl. 10, fig. 3) where the cells are flattened against the forming dentine wall. The arrangement of the fibres with spaces parallel to the long axis of the tooth, indicative of fluid pressure are seen in the dentine of the Mackerel (Pl. 10, fig. 5). Radiation of pressure from the pulp as represented by the appearance of the dentinal tubules is seen in most histological sections (Pl. 3, figs. 4, 7, 9 and many others). The cylindrical form is evident in sections transverse to the tubules which are seen as rings (Pl. 6, figs. 1, 2, 6). The genetical factor is important, for parts of dental germs grown *in vitro* have the form of normal development in spite of a changed environment, with absence of pressure of filtration from blood capillaries although the local osmotic forces are probably closely similar (Glasstone, 1955).

SOME FUNCTIONS OF DENTINE

Dentine has undergone great changes in function since its presence as a protective and supporting calcified tissue upon the shield of the earliest known vertebrates. Dentine with this function is also found in scales of fishes of a primitive type. The rapidly moving teleost fishes have the scales so reduced that only a very thin calcified layer is present; there is lamination of the scales, as with all compact calcified connective tissues, but without evidence of dentine structure, except for being acellular and avascular. In terrestrial animals dentine is present only in teeth which are regarded as modified scales. The evolution of scales to teeth is commonly accepted but, if confirmed, the altered function is most complex. The change is from a passive to an active state, associated with uses as tools, weapons, and occlusal stresses, when teeth are situated upon the jaws. The modifications of scales into gill rakers or into sharp teeth for seizing prey is more readily conceived than the complex teeth for triturating food, although it occurs early with teeth for crushing shell-fish as in Edestidae, Heterodontidae and other elasmobranchs where the scales and teeth are so similar.

Little work has been done associating the changes in structure with functional variations ; what difference is there in the dentine of a canine as a fighting tooth and that of a tooth resisting the pressure of biting food, which should also provide variations according to the nature of the diet in an animal ? There are obvious differences in the structure of the dentine of fishes and mammals although so similar in their mode of development. The associated functional differences should provide a most interesting field of study.

The avascular and acellular nature of dentine may have arisen as a less vulnerable superficial tissue, the risk of haemorrhage following injury and possible infection is avoided as with an epidermis.

The functional value of dentine has been little studied, but two features are of particular interest, one its sensitivity, especially recognized in human dentine, the other its elasticity.

DENTINE AND SENSATION

One hundred years ago John Tomes endeavoured to ascertain the path of sensation in a human tooth without reaching a conclusion, and so far no satisfactory conclusion has yet been obtained. Sensation in dentine of teeth, other than human, is hardly more than assumed. Histologists working on human dentine have been able to show nerve fibres in the predentine and dentine near the pulp. They are demonstrated little beyond this region in spite of the careful investigations of Mummery (1912, 1918, 1924) and others ; the many opinions expressed are summarized by Wellings (1940). Many investigators, including Mummery, conclude the nerve fibres pass along the dentinal tubules to terminate beneath the enamel. That nerve fibres pass into the dentine matrix is discussed by Cocker & Hatton (1955) who refer to Wellings' summary and the work of Bradlaw (1939) and Powers (1952). They say : " In many sections where the predentine contained numerous fine fibres, some of these could be traced into the calcified dentine where they are very soon lost ".

No one has described a nerve receptor in dentine.

Dentine in man is sensitive, and in the region of the pulp astonishingly painful. There is no physiological explanation of this acute response to a stimulus which, on account of its situation, can only be appreciated by injury. The writer has come to the conclusion that the nerve receptors are situated in the dentine close to, or at the pulp surface, and that the elasticity of the dentine is responsible for their stimulation. Very sensitive nerve terminals are needed to appreciate the significance of variations of tension and pressure in dentine, and to an animal whose teeth are essential to its survival, a consciousness of the nature of a substance bitten upon or contacted is of vital importance.

Human dentine exposed by a fracture can be quite sensitive if near the pulp but is often painless although it may become painful. Nerve fibres are thought to be present in the dentine on account of this response.

The conclusion is reached that the nerve receptors are situated in the region of the pulp surface and their presence beyond this zone is doubted although corroborative evidence is needed. Nerve receptors near the pulp surface may receive impulses transmitted by variations of fluid tension in the dentinal tubules associated with slight changes in the matrix.

Clinical experience of a dentist demonstrates a definite response to a drill upon dentine immediately beneath the enamel but, when continued, the tissue beneath is less sensitive. Fluid tension in the tubules is reduced when the tubules are opened and transmission altered. It must be remembered the fluid content is colloidal, so that although tension is altered, escape of fluid does not occur freely, particularly from the very fine terminals. Many other clinical experiences need to be explained, like the finger nail upon an exposed toothbrush erosion cavity at the neck of the tooth, formerly so common when gritty tooth powders were used; it is suggested this is due to electrical changes on account of the varying reactions of different stimuli. The functional sensitivity of dentine is hardly explained beyond response to injury with which thermal variations are included. Exposed dentine responds to variations due to osmosis or dehydrations by solutions, like sugars. The formation of secondary dentine due to attrition, is seen as a normal process in many animals, probably as a sensory response. The diminished sensation after injury or with advancing age, is associated clinically with reduction of the tubules by what is described as calcification.

Sensation at the pulp surface is the most favourable site for the reception of stimuli from variations in tension due to elasticity of the dentine, the changes in pressure are better received collectively in this position than by local stimulation near the surface. The fine channels of the dentine surface would convey fluid variations of pressure with a corresponding change in the larger tubules nearer the pulp. This change would correspond with the variation recorded by a hydrostatic or Bramah press. The fine tubules are favourably placed for detection of change in the surface dentine and the presence of interglobular spaces may be significant.

The acuteness of the pain in response to stimulation at the pulp surface of human dentine is probably not exceeded in any other part of the body. That this sensitivity is not explained is surprising but this is probably because it is recognized only pathologically and has no known physiological significance. Beyond clinical experiences no experiments have been conducted upon sensation in dentine at the pulp surface.

The interglobular spaces in the surface dentine beneath the enamel have attracted attention as possibly being associated with tooth sensation. The presence of tissue fluid in these spaces may be significant, Mummery (1924), as many have done, questioned their association with nerve terminals, he comments (p. 242) :

“ The contents of the interglobular spaces are usually granular, but sometimes appear quite clear. It was noticed by Tomes that in caries of the dentine the tubules filled with micro-organisms are more expanded or dilated within the interglobular spaces, as they probably meet with less resistance than in the calcified dentine.”

The penetration of dyes defining the spaces is seen in some sections, although free dissemination is not achieved (Pl. 9, fig. 4). The flattened areas are larger than the diameter of the tubules and so not readily reached by the fluid, but outlining the spaces by dyes indicates communication with the tubules. Mummery's comment, that the dentine tubules pass the interglobular spaces, was probably due to the different plane of the very thin spaces and tubules in a section.

Mummery (1924, p. 229) describes the basal layer of Weil as "being entirely occupied by a dense plexus of delicate nerve fibres forming the deep plexus or plexus of Raschkow". The presence of these fibres in relation to the dentine at the pulp surface may have significance. The basal layer of Weil is well shown in Pl. 2, figs. 1, 2.

ELASTICITY OF DENTINE

Elasticity is a property of dentine very well known to physicists, and makers of ivory billiard balls, but is hardly recognized by zoologists or dental surgeons. Investigations into the physical properties of dentine have been carried out, but little recorded information can be obtained, and the makers of billiard balls informed me that plastic materials are used now in place of ivory. Comparing favourably with teak but less so with steel, which is more uniform in structure, dentine is one of the most elastic substances. The investigations upon the physical aspects of dentine have been carried out chiefly upon dried ivory, but to the present study this important aspect of dentine applies to properties in a living animal, and except for Black (1895) few experiments have been conducted on fresh material. In his experiments upon dentine of human non-carious and carious teeth Black demonstrated its elasticity, observing a distortion and restoration of from 5 to 8 per cent. He records using varying pressures up to 350 lb. upon a point 1/800th of a square inch, and upon dentine of a similar thickness and states that few fractures were produced. The results obtained he expressed in prepared tables.

The elastic properties of fresh dentine opens up a wide field for further study. Dentine is not a uniform structure and its elasticity needs to be considered from the nature of its matrix and permeating tubules or spaces. Variation will be found to be present in the dentines of different vertebrates and in the individual teeth of an animal. At present elasticity of dentine in the teeth of large mammals is best known, if only in a limited degree as ivory.

The functional value of the elastic properties of dentine is not known. The resistance to deformation due to repeated stresses upon teeth is obviously enhanced by an elastic property with complete return to its original form. It is now suggested that the variation of tension in the dentine is conveyed by its elasticity to the nerve terminals near the pulp surface. The evidence although limited, seems sufficient to come to the important conclusion that the acute sensibility of the nerve terminals in the region of the pulp surface record changes in the dentine.

I am indebted to Dr. Grant and Professor Roberts at the Physics Department of the Middlesex Hospital for investigations upon the physical properties of dentine which are being continued.

The length of the paper and the many aspects discussed almost demand an apology but negative statements are rarely of much value without alternative positive observations. The author having come to the conclusion cytoplasmic processes from the odontoblasts are not present endeavoured to give some positive conclusions.

DISCUSSION

The great advance in knowledge of the components of the connective tissues, with a general application to all forms including dentine, increases possibilities for investigation. The different acellular calcified connective tissues to which the name dentine is given seem to be justifiably grouped but similarity of development should be shown. In distribution they are widely divergent between that of the early aquatic agnathic vertebrates as surface structures and of the teeth of terrestrial animals providing an extensive range for study, particularly in determining their relations to one another.

Tubular dentine apparently precedes other forms of dentine, and its relation to other forms and to bone, in particular to dermal bone of the aquatic vertebrates, presents a field of investigation for closer correlation of different workers.

The presence of a syncytium in bone is doubted, and should this be confirmed, bone is more intimately related to dentine in its development, presenting an interesting study.

Fully developed dentine with its reduced metabolic interchanges, and being acellular, is a special and of a more inert form than other calcified connective tissues. Its functional properties have been little studied and its elasticity in teeth and the acute response in man to stimuli near the surface of the pulp, if correlated as suggested in this paper, demand further study. C. Tomes (1923, p. 87) expresses doubt upon the transmission of a nerve stimulus through fluid in the dentinal tubules. The relative arrangement of the component structures of the matrix due to variations of pressure and tension in the tissue fluid needs much fuller investigation. Whatever variations occur in the colloidal state of the components of the tooth tissues during development and later, they are derived from the fluid blood stream and any return is as a fluid content of the lymphatics or veins.

Odontoblasts recognized as fibrogenetic cells forming the matrix and not having cytoplasmic processes in the dentinal tubes or spaces present an altered concept in the study of dentine, both in structure and function, also in pathological lesions.

With the many improved modes of investigation the knowledge of dentine will be greatly increased. A more comprehensive study of the structure and functions of dentine is needed, with a closer co-operation between individual workers upon the forms of dentine so differently situated.

SUMMARY

1. Dentine is recognized as an acellular and avascular calcified connective tissue matrix permeated by fine channels containing tissue fluid.
2. The distribution of structures which fulfil this description of dentine is very wide, in fact it is present in all vertebrates with only one or two exceptions. It is seen in the shield of the ostracoderms, the earliest known vertebrates, in the scales or superficial calcified mesenchyme tissues of early fishes and in all teeth, to which in terrestrial animals it is restricted.

3. Kindred structures to which a qualifying word is added to that of dentine, such as osteo-dentine, are not discussed. Of the many names for the form of dentine described here that of tubular dentine is used.

4. The greatly increased knowledge of the components of the connective tissues and recognition of a possession of basic properties in a closer degree than formerly, has advanced the interpretation of structural and functional features and certainly applies to dentine. Reference is made to the uncertain relation of reticular fibres to those of collagen.

5. The former conception of cytoplasmic processes from the odontoblasts occupying the dentinal tubules is shown to be erroneous, so that tooth-dentine, composed of a matrix or ground substance permeated by tissue fluid, is nearer in structure to other forms of connective tissue.

6. The statement by Tomes is quoted showing that he is misinterpreted if the dentinal fibrils in the tubules described by him are regarded as processes from the odontoblasts. The contents of the dentinal tubules are now recognized in histologically fixed specimens as coagulated colloidal components of the tissue fluid.

7. Odontoblasts, like fibroblasts, are fibrogenetic; they give rise to the collagen fibres and mucopolysaccharides forming the dentine matrix with which they are directly connected. Granules are present in the cells and in the forming dentine matrix, a continuity is such that distinction between the end of a cell and its connection with the predentine matrix cannot be determined and there is no evidence of a cell membrane in this position.

8. Collagen fibres, completing the walls of the dentinal tubules in the formation of the dentine matrix have been mistaken for the fibrils of Tomes.

9. The opinions expressed by many authorities upon the contents of the dentinal tubules are discussed, the statements are made almost entirely upon human dentine and laboratory animals. A study of the tissues over a wider field was undertaken, the teeth of vertebrates ranging from fishes to man are discussed and the arrangement in the diphyodonts and polyphyodonts considered.

10. Development of tooth-dentine is described in relation to the changed conception of its structure, and comparisons are made with the interpretations by other authorities. The development of other forms of tubular dentine is little known and is assumed to resemble the production of tooth-dentine.

11. The relation of the blood capillaries to the odontoblasts forming a Vaso-cellular barrier is described and comparison made with bone formation. The production of dentine beyond this barrier gives rise to the characteristic acellular and avascular structure.

12. Attention is drawn to the importance of the pressure and variation of tension in the tissue fluid in determining the arrangement of the components of the matrix during development and the maintenance of the tissue fluid spaces, in mammalian dentine as tubules which are cylindrical due to fluid being laterally contained.

13. During the development of dentine evidence is present indicating pressure in the tissues within the rigid layer of the internal dental epithelial cells of the enamel organ which determines their arrangement.

14. The uniform appearance of dentine is due to the products of the odontoblasts blended and being moulded together by the tissue fluid pressure in the tubules or tissue spaces. There is no evidence of individual production of the matrix by an odontoblast in histological sections, the tubules cut transversely appear as empty rings in a homogeneous matrix.

15. The functional importance of elasticity is commented upon in relation to sensation in teeth. The terminal nerve receptors are regarded as situated near the pulp surface and not at the outer aspect of the dentine.

16. Tooth-dentine is discussed almost entirely as other forms of dentine are too little known and generally are assumed to be similar in structure and probably in development. This is accounted for largely because nearly all forms in a satisfactory state of preservation are obtained with difficulty, particularly in the developmental stages.

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PLATE 1

PLATE 1

Sections of fragments of shields and dermal bones of the earliest known vertebrates from the Colorado Ordovician deposits estimated as 400,000,000 years ago. Prior to the evolution of jaws. Cut for Sir A. Smith Woodward (1921) at the British Museum (Natural History). Photographed by courtesy of Dr. Errol White.

Fig. 1. British Museum Slide P. 10624. c. (x 54)

Three denticles cut vertically showing radiating tubules. The appearance resembles that seen in scales of fishes as demonstrated by Williamson (1849-50). Lower in the field the denticles and the spaces from which the channels radiate are cut transversely. The denticles are probably upon the outer aspect of a shield. Enamel is absent differing from fig. 4. where it appears to be present.

Fig. 2. British Museum Slide P. 10624. b. (x 385)

Higher magnification of a "denticle" than in fig. 1. Tubules radiate from the upper part of what resembles an extension from the cornu of a pulp-like projection. The surface of the denticle or dentine-like structure is indicated.

Fig. 3. British Museum Slide P. 10624. a. (x 385)

Radiating tubules with an appearance closely resembling tooth-dentine although before teeth are known to have evolved. The arc of dark spaces resembles in appearance the "granular layer of Tomes" beneath cementum. Projecting ridges or cones are cut across at the free surface.

Fig. 4. British Museum Slide P. 10624. a.

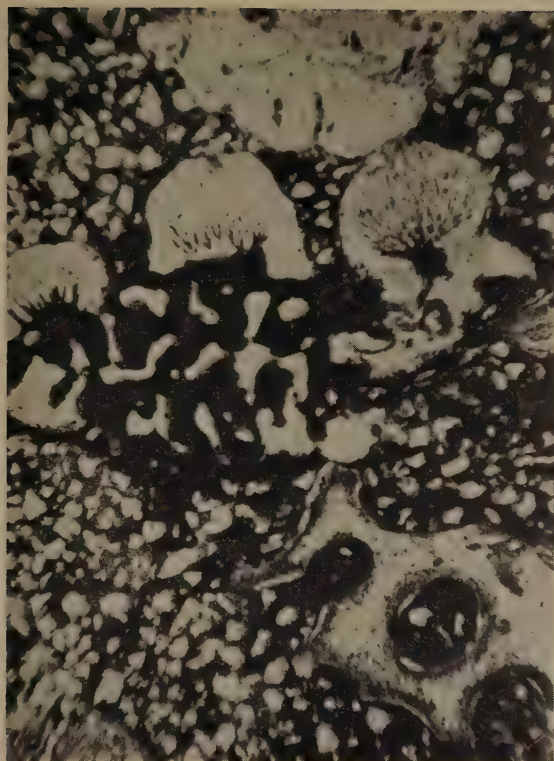
Tooth-like structure with an appearance of enamel and dentine as seen in the arrangement of a crushing tooth. On the right there are lamination-like grooves or fibres but are probably artefacts as they cross the break in continuity with the tissue beyond which is probably akin to bone of attachment. The dark area on the left side suggests radiating tubules. The wide open base is characteristic of a polyphyodont tooth in a fish and the calcified tissue on each side at the base is closely similar to the attachment connecting a tooth to the bone in a fish.

The structure in each photograph presents an appearance which would be generally accepted as dentine, being tubular, acellular and avascular. The thickness of the layer of dentine seems to be wider than the dentine in more recent structures. The same comment applies to the enamel-like layer in fig. 4.

Soft tissues covering these calcified structures are unknown although almost certainly present. We are equally ignorant of the tissues that preceded these highly complex structures, a long period for their evolution was obviously necessary.

NOTE: For abbreviations see Text-fig. 1, page 2.

Details in many sections illustrated are seen better with a lens (reading glass).



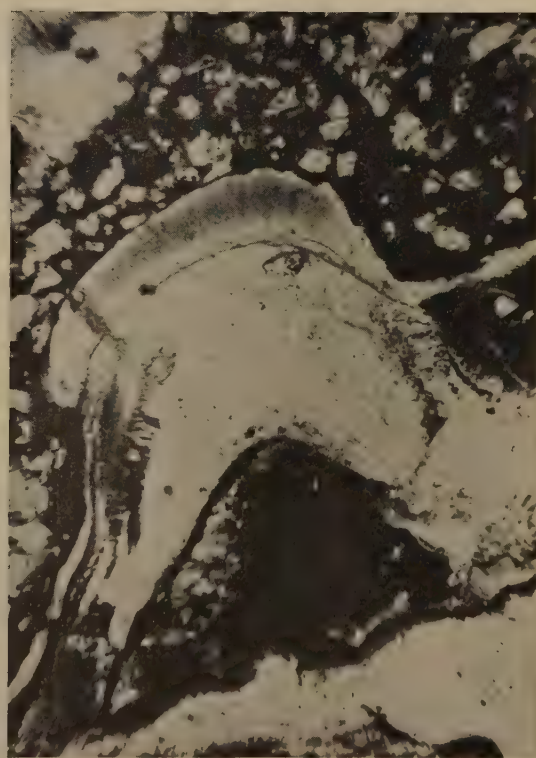
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PLATE 2

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PLATE 2

Fig. 1. Rat Molar. Masson. (x approx. 480)

Formed and developing dentine with odontoblasts. Odontoblasts and projecting fibres red passing to red stained matrix. Contrast in staining due to phases of development, red strands probably collagen fibres and blue granular tissue of the predentine precollagenous. They show as columns in section although in transverse section appear as homogeneous matrix surrounding the tubules. The cells, so frequently displaced, are held in position by the firmer fibres (red). The pulp cells below the clearer "basal layer of Weil" are red and the intercellular substance pink. Knowledge of the response of the tissues to stains is still obscure as with the tubules and matrix stained blue in the dentine.

Fig. 2. Rat. Masson. (x approx. 1600) Higher magnification of fig. 1.

Red and blue granules becoming fibres as "processes" from the odontoblasts pass to the matrix. The red stained cells, collagen fibres of the predentine and the dentine matrix are in marked contrast with the blue predentine. The tubules in the dentine are only just indicated but are distinct in the predentine where the forming matrix is defined on one side by the red collagen fibres which pass to the dentine matrix forming the wall of a tubule. See fig. 1.

Beneath the odontoblasts an acellular space, the "Basal layer of Weil" (1887) is probably a tissue fluid space, Mummery (1924) says it contains a plexus of nerves.

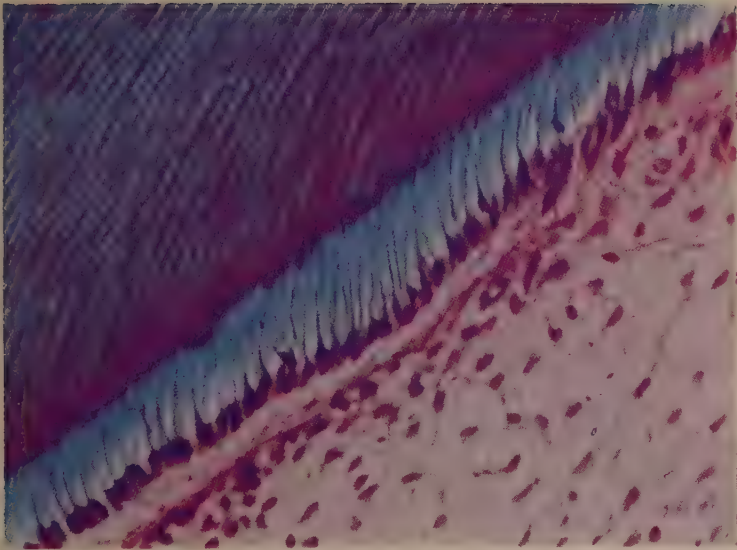
Fig. 3. Mangabey Monkey. Azan. (x approx. 480)

Clear dentine tubules with pink stained matrix around them. The characteristic narrow rounded ends of dark blue stained predentine are clearly shown; they are completed by continued addition of fibres related to odontoblasts, formerly believed to be cytoplasmic processes. The red odontoblasts and collagen strands pulled partly away from the forming dentine alone are stained. Features not evident here are shown in Pl. 5, fig. 6. from the same section.

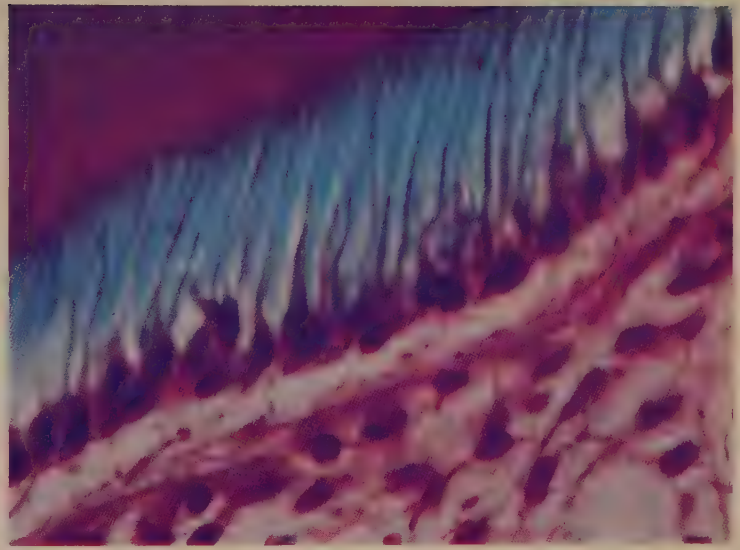
Fig. 4. Guinea Pig. Masson stain. (x approx. 480)

Capillaries with erythrocytes and endothelial cells among well formed "square ended" odontoblasts. Dentine matrix blue with connections to odontoblasts. Probably little gross displacement. The contraction of the cell cytoplasm gives an appearance of a basement membrane. Such an arrangement is only evident in sections where the odontoblasts are square ended with a contrast in fixation and staining at a delicate junction of cell and forming tissue. Enamel red with blue surface where ameloblasts are pulled away. The anomaly of the staining needs to be explained.

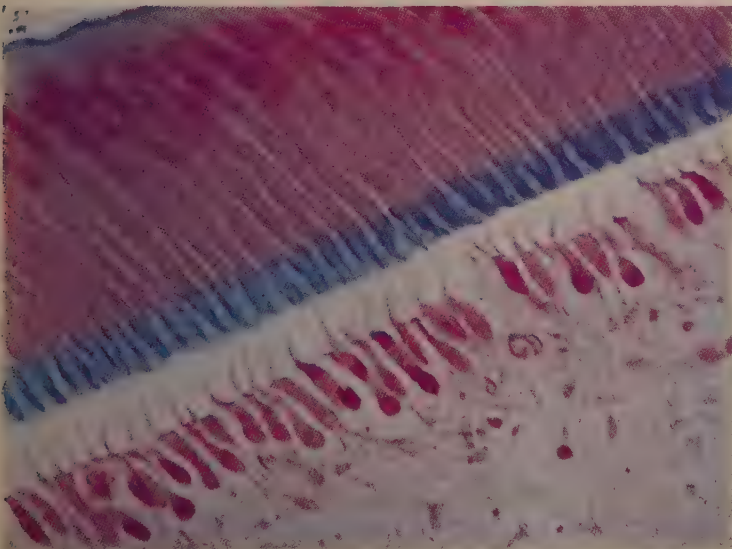
Photographs in colour taken at the Anatomical Dept., Middlesex Hospital by Mr. P. Runicles.



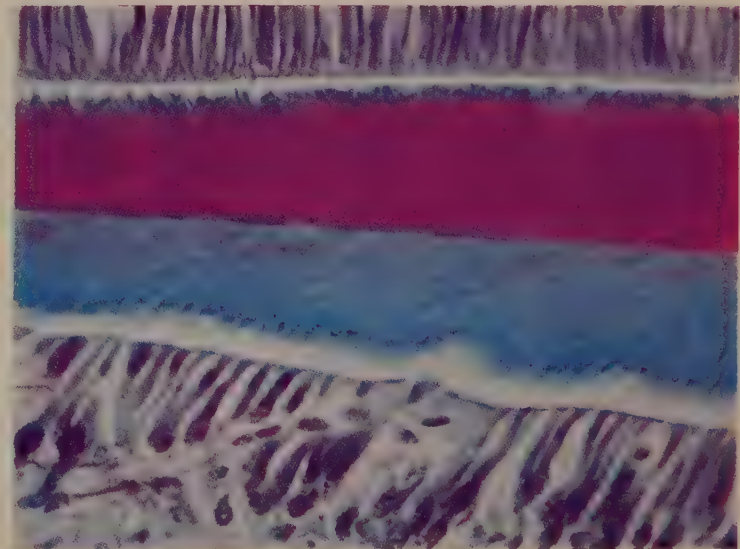
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PLATE 3

PLATE 3

Fig. 1. *Homo sapiens* (Milk Molar). (x 385)

Fig. 2. Armadillo. (x 385).

Fig. 3. Gaboon Viper. (x 385)

The above three ground sections showing the resemblance in widely different animals of the dentine matrix and tubules to one another and to decalcified sections as in figures 4. marsupial, 5. lizard, 7. fish, 8. deer, 9. insectivore.

Fig. 4. Black Wallaby. H. & E. (x 385)

Collagen fibres from associated odontoblasts passing to the dentine matrix. Characteristic parallel dentinal tubules as in ground sections figs. 1, 2, 3, show their communications with tissue fluid spaces of pulp.

Fig. 5. Agama. H. & E. (x 385)

Empty appearance of tubules radiating from pulp and continuity of odontoblasts with matrix in an acrodont lizard. A pleurodont lizard, Pl. 8, fig. 5.

Fig. 6. Agama. H. & E. (x 1000) (from same section as fig. 5.)

The highly magnified obliquely cut section shows the unequal size of the odontoblasts and the area of the forming matrix. In other sections they do not correspond exactly although they may appear to do so varying with the plane in which they are cut, see Pl. 4, figs. 1, 2, 3, 4.

Fig. 7. Minnow. H. & E. (x 385)

Odontoblasts connected with predentine matrix. Tubules pass to intercellular tissue fluid spaces of pulp and radiating from the pulp show curvatures which being cylindrical are unduloid when their length is three times their width according to d'Arcy Thompson, see fig. 9.

Fig. 8. Muntjac. H. & E. (x 385)

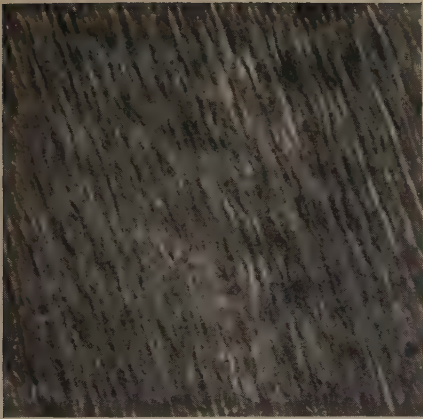
Pulp tissues pulled from predentine with odontoblasts still connected to the matrix by bundles of collagen fibres. Open tubules continuous with intercellular spaces of pulp. The absence of cytoplasmic processes from the odontoblasts in the tubules and the connection of collagen fibres to the matrix is clearly demonstrated. Compare with figure from Tomes' paper (Pl. 4, fig. 4).

Fig. 9. Common Shrew. Mal. (x 385)

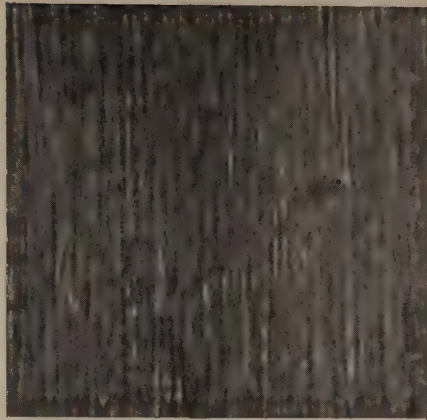
Matrix, dentinal tubules and pulp in a mammal. Curvatures of tubules indicate pressure of tissue fluid radiating from pulp as in fig. 7. Very small odontoblasts could hardly supply cytoplasmic processes to occupy all the tubules. Section is referred to in text as showing proportion of tubules to matrix.

Fig. 10. Lamb. Bielschowsky-Maresch. (x 385)

Section demonstrating the continuity of the dentine matrix with odontoblasts through granules of predentine without any suggestion of cytoplasmic processes passing to the dentinal tubules. Where the cell ends and the predentine matrix commences is indistinguishable, see Pl. 4, fig. 5.



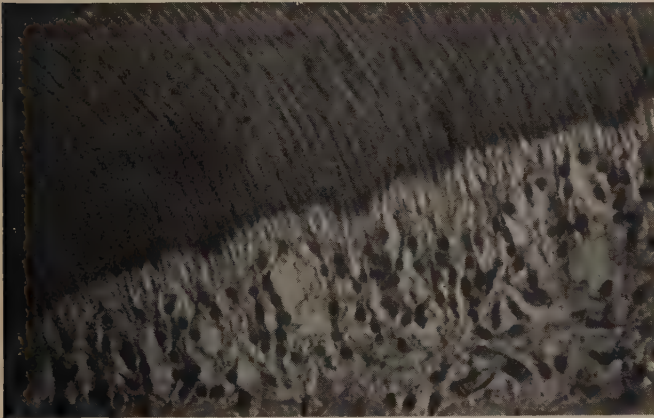
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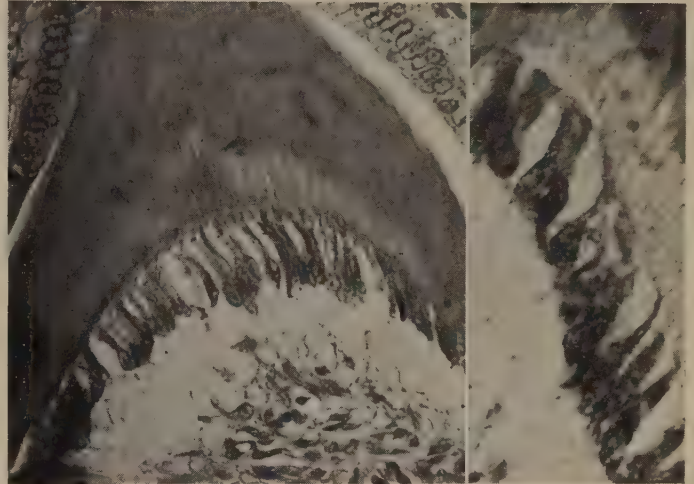
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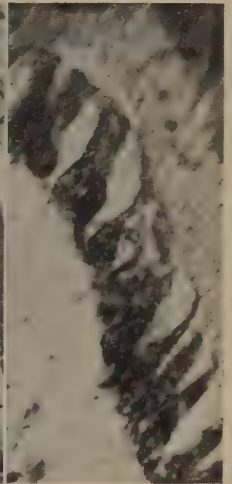
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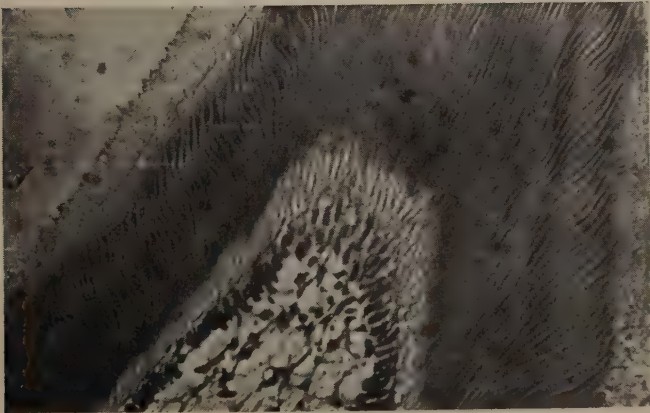
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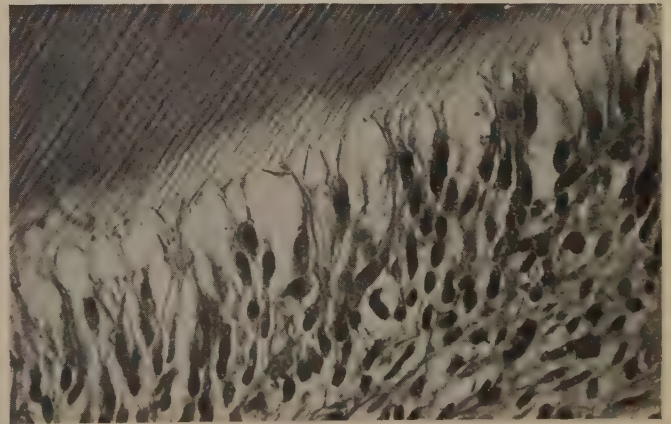
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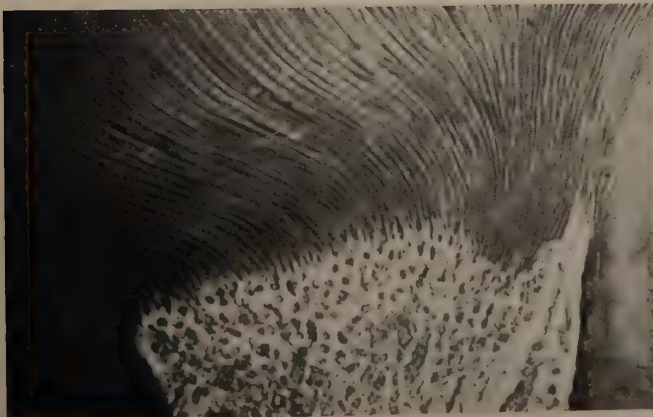
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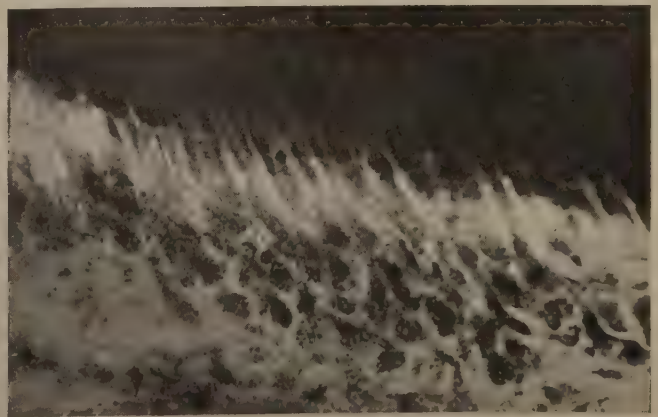
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PLATE 4

PLATE 4

Fig. 1. Lamb. H. & E. (x 165)

Square ends of odontoblasts shown. Section is oblique and disproportion of size of cell to forming matrix emphasized. Seen also in figs. 2, 3, & 4.

Fig. 2. Foetal Lion. Mal. (x 385)

Squared ends of odontoblasts with fibres to matrix of very narrow predentine layer. The torn internal dental epithelial cell layer has remained intact in spite of displacement, a relationship maintained with much greater disturbance. This rigidity is an important feature of early development in opposing tissue fluid pressure, see page 32.

Fig. 3. Bull Frog. Silver Stain (Lillie) (x 385) Dr. Wellings' Section

Squared ends of odontoblasts against granular matrix of predentine. Tubules distinct with clearer appearance than usual in predentine where fibres passing to the walls interrupt definition, see figs. 1, 4. Compare Pl. 7, fig. 1.

Fig. 4. Kitten. Injected Specimen. H. & E. (x 165)

Clear appearance of tubules in dentine, dark margins have been regarded as fibrils. Finest capillaries not reached by injection as in Pl. 8, fig. 8. of same series. Compare predentine of fig. 3.

Fig. 5. Lamb. Robb Smith Silver Preparation. (x approx. 1000)

Cytoplasm of odontoblasts directly continuous with predentine matrix, no definition between cell and matrix. Each composed chiefly of granules, little evidence of fibre formation in early forms probably destroyed during decalcification. Granular formation resembles recent observations upon osteoblasts. Continuity of tubules and intercellular spaces.

Fig. 6. Lamb. Bielchowsky Silver Stain. (x approx. 1000)

A single odontoblast with deeply stained nucleus at pulp end and granules forming fibres without definition of cell boundary from matrix. Continuity of granules and matrix seen below with intervening tubules.

Fig. 7. Copperhead. Bielchowsky Silver Stain. (x approx. 1000)

Somewhat oblique section, granular cytoplasm of odontoblasts continuous with matrix of developing dentine. End of cell and commencement of predentine cannot be determined.

Fig. 8. Australian Tiger Snake. Masson. (x approx. 1000)

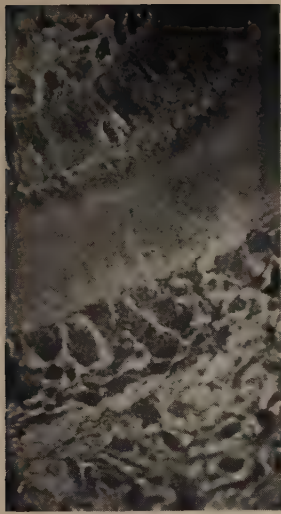
Odontoblasts obliquely cut, granular cytoplasm directly continuous with predentine matrix without distinction between odontoblast and matrix. Tubules and intercellular spaces coincide as in fig. 7.

Fig. 9. Lamb. H. & E. (x approx. 1000)

Odontoblasts cut obliquely and cells appear wide, granules in cytoplasm almost defining its end continuous with matrix. Absence of cell wall between cell and forming matrix is surprising but seen constantly in sections. Forming collagen fibres are indicated.

Fig. 10. Kitten (9.8 cm.) Schiff. (x approx. 1000)

Earliest development of predentine immediately beneath basement membrane. Cells of I. D. E. and odontoblasts approximately at right angles to the basement membrane, a constant feature. Fine granules and delicate fibres are evident and directly related to odontoblasts but whether belonging to cell or the early forming predentine cannot be determined. The spaces between the odontoblasts suggest the formation of the tubules.



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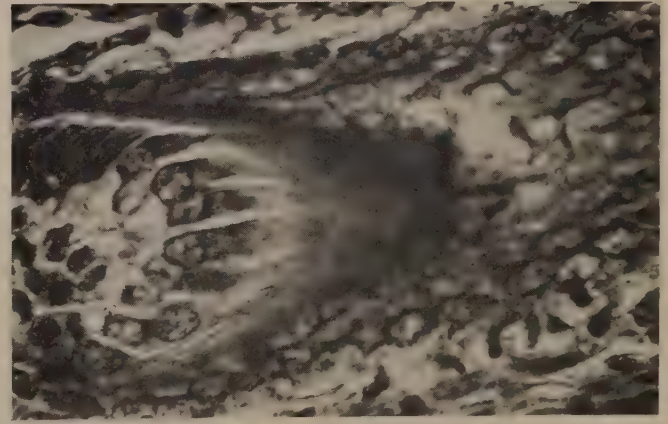
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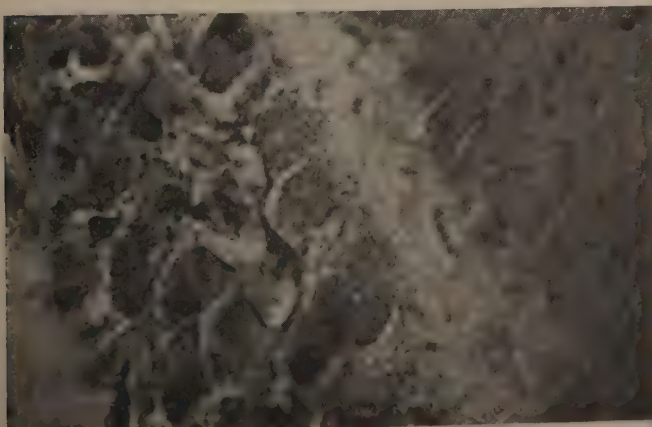
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PLATE 5

PLATE 5

Fig. 1. Grey Gurnard. Mal. (x 385)

Tubules clearly defined, more noticeable in formed dentine than predentine in which fibres cross in process of forming walls of the tubules under the pressure of the contained tissue fluid.

Fig. 2. Grey Gurnard. Mal. (x approx. 1000)

Same field as fig. 1. Absence of definition of where the cell cytoplasm ends and the predentine commences, a constant feature in dentine development. The most noticeable "tubule" especially focused has a long granular process from an odontoblast passing to the matrix forming the wall of the tubule. Seen on the right in fig. 1. where details also evident.

Fig. 3. Chimpanzee. H. & E. (x 385)

Section cut at the Dept. of Anatomy, London Hospital by courtesy of Professor J. D. Boyd. Border of the dentine. Tubules clear, some over matrix, section oblique and thick. Dark tubule margins, not in focus at side of section, suggest dentinal fibrils, compare Pl. 6, figs. 1, 2, 3, 4. Rounded narrow ends of matrix a common feature, as addition to the matrix occurs by progressive building up of the wall of the tubule. Odontoblasts not in the same plane of section.

Fig. 4. Reproduction of de Morgan's *drawing*, Tomes (1856)

Pulp tissues pulled from dentine, projections regarded by Tomes as extensions of the soft fibrils occupying the dentinal tubules. Tubules continuous with containing walls of matrix. No evidence of cytoplasmic processes from odontoblasts, nor was it suggested by Tomes.

Fig. 5. Tiger (2 days old). H. & E. (x 445)

Pulp tissues pulled from predentine leaving collagen fibres of matrix projecting, resembles fig. 4, but a photograph and not a drawing.

Fig. 6. Mangabey Monkey. Azan. (x 385) (Same section as Pl. 2, fig. 3 in colour)

Processes from odontoblasts focused to show them passing to the walls of the dentinal tubules and the narrow ends of the matrix to which the fibres are being added. The appearance suggests processes entering the tubules but contradicted by careful examination. Photograph in colour shows characteristic empty appearance of the tubules. A wonderfully marked contrast in photographs of the same section (Pl. 2, fig. 3).

Fig. 7. Cat. W. & VG. (x 385)

Adult, formed dentine, matrix and tubules distinct. Individual bundles of fibres in matrix directly continuous with those of pulp, not in such close proximity to the cells as when developing. Tubules and intercellular tissue spaces are in direct communication.

Fig. 8. Cat. W. & VG. (x approx. 1000) (From the same section as fig. 7)

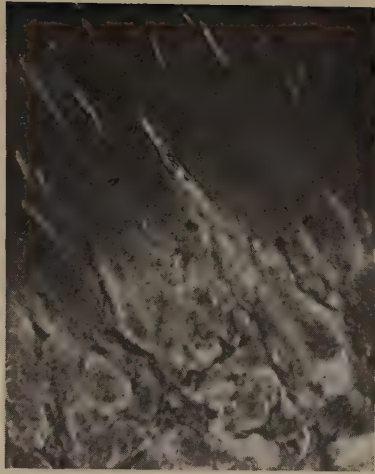
Relation of collagen fibres to odontoblasts. Blood capillaries seen here with the odontoblasts form the Vaso-cellular barrier.

Fig. 9. Human. W. & VG. (x approx. 1000)

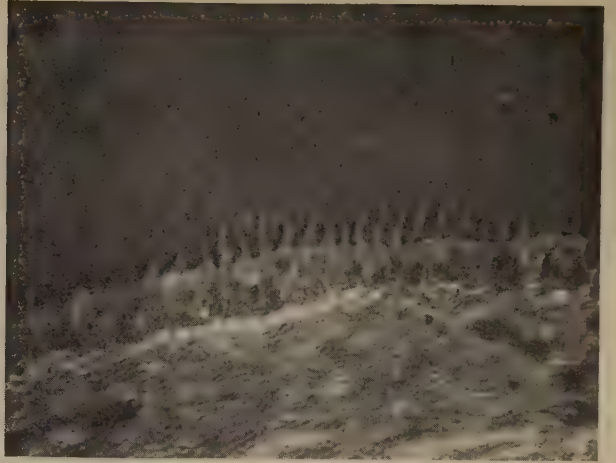
Pulp tissues pulled from dentine leaving bundles of collagen fibres continuous with those of the matrix, fibres swollen from prolonged immersion in ten per cent solution of nitric acid.



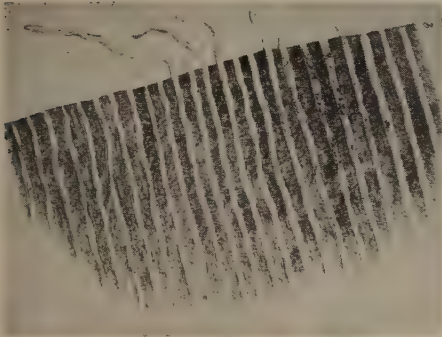
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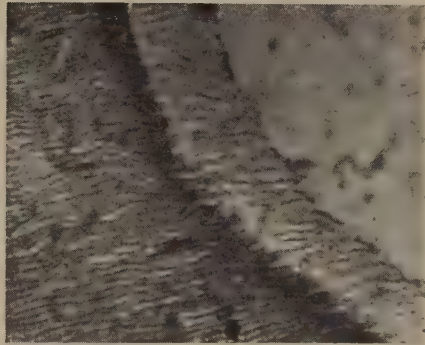
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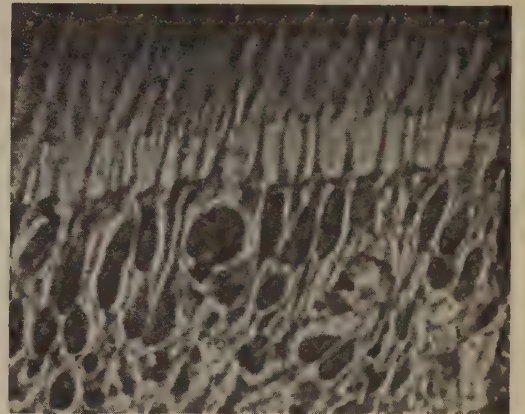
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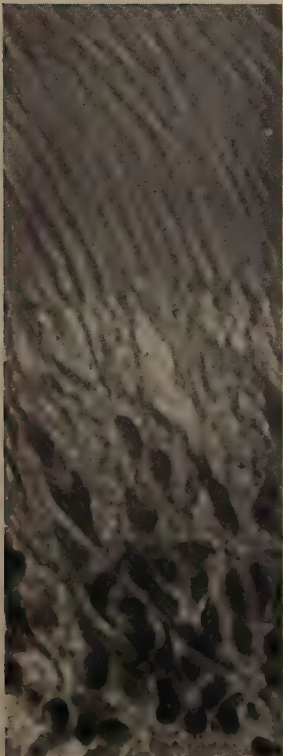
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PLATE 6

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PLATE 6

Fig. 1, 2. Human. H. & E. (x 165)

Two photographs of a section transverse to dentine tubules, the *same field* with variation of focus, a slight turn of the fine adjustment. Fig. 1 tubules more in focus, appear as clear rings, fig. 2 "dots" are seen in place of tubules and usually described as dentinal fibrils cut across.

A transverse section of dentine showing rings indicates a cylindrical form of the tubules, supporting the idea of pressure radiation from pulp. Uniform appearance of the matrix without evidence of production by individual odontoblasts is noticeable in all sections.

Fig. 3, 4. Rat. H. & E. (x 385)

Obliquely cut tubules, the *same field* seen with variation of focus.

Fig. 3 more accurately focused tubules appear empty.

Fig. 4 with change of focus, a dark margin to tubules, described as dentinal fibrils. Appearance varies between crescent of tubule cut obliquely or complete "fibril" if margin of tubule straight.

Fig. 5. Two-toed Sloth. H. & E. (x approx. 1000)

Highly magnified dentine tubules cut longitudinally, appear empty or with fragmentary contents. Plane of section and focus affect appearance as where obliquely cut cone-shaped dark area is seen over a tubule. Sections of tubules with high magnification are difficult to interpret. In the sloths where osteodentine occupies the pulp cavity as in fig. 6 there are no odontoblasts to supply processes.

Fig. 6. Three-toed Sloth. W. & VG. (x 385)

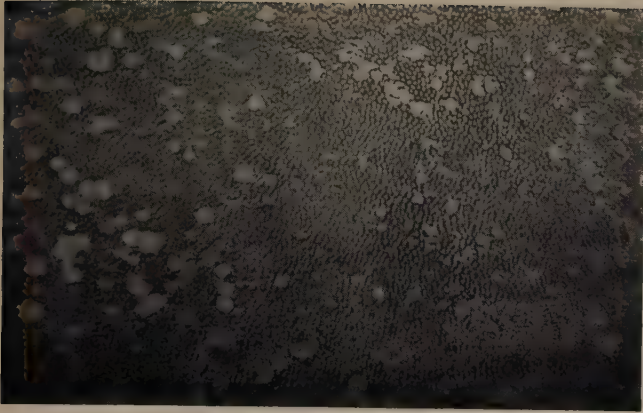
Where pulp replaced by osteodentine, cytoplasmic processes from odontoblasts cannot be present see fig. 8. Tubules cut transversely show a central "dot", not disposed of by focus is regarded as coagulated colloidal content of the tissue fluid, possibly more concentrated with tissue fluid connection with pulp altered.

Fig. 7. Three-toed Sloth. W. & VG. (x 165)

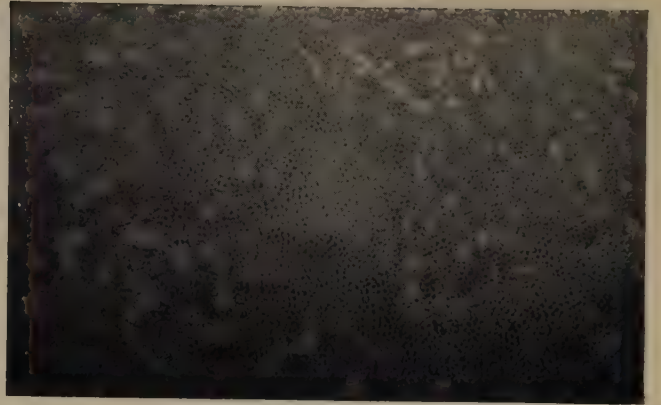
Lower end of side of tooth giving relationship of dentine to cementum on the outside with periodontal membrane just seen at the top corner. Tubular dentine in centre and below osteodentine *which* has replaced the pulp, small fragment of pulp is seen in angle between these. Surprisingly little variation in appearance of dentine opposite pulp or osteodentine, the latter a little darker, probably a fault in photograph.

Fig. 8. Three-toed Sloth. W. & VG. (Low power.) Photograph by Mr. Sawyers.

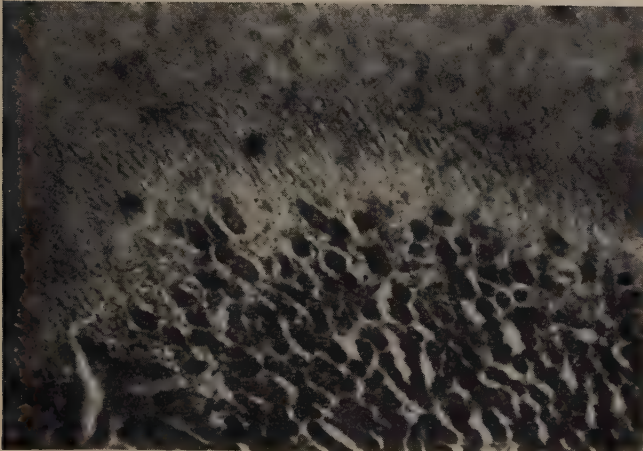
The tooth, devoid of enamel in edentates, has a rough biting surface due to difference in hardness and unequal wear. Cementum dark is outside a lighter band of dentine which encloses the osteodentine occupying the greater part of pulp cavity. No odontoblasts present where the pulp is replaced by osteodentine and the presence of cytoplasmic processes in the dentine tubules is impossible.



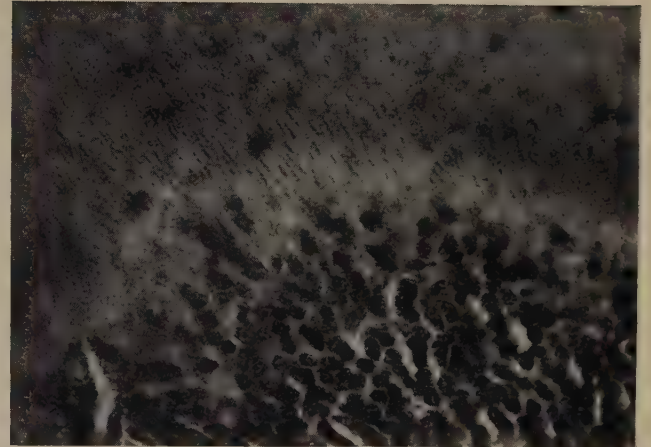
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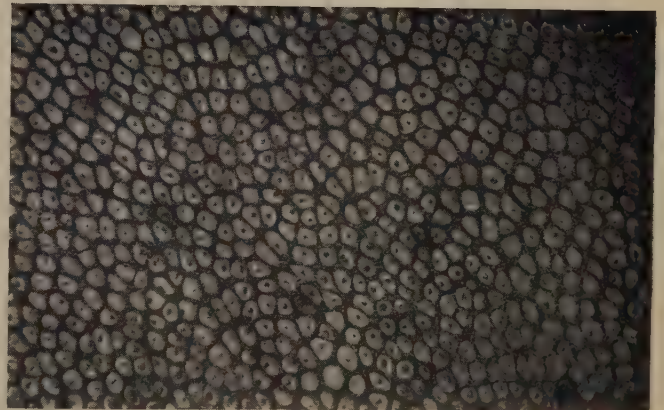
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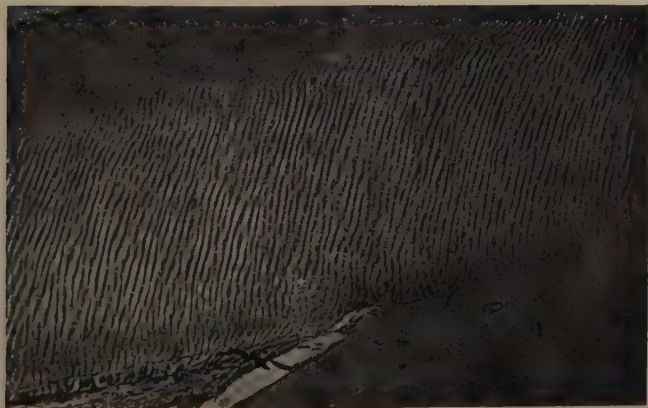
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PLATE 7

PLATE 7

Fig. 1. American Bullfrog. H. & E. (x 385) Dr. A. Wellings' section.

Odontoblasts directly connected with wide predentine matrix. Intervening channels or tissue spaces continuous with those of the pulp. More resemblance to fishes than mammals.

Fig. 2. American Bullfrog. H. & E. (x 385) Dr. A. Wellings' section.

Deepest part of a dental lamina showing the *earliest* indication of change in the cells of the internal dental epithelium and mesenchyme for production of a tooth. Differentiation of the epithelial cells, near to the end of a dental lamina, occurs on the face adamantine of Pouchet & Chabry and opposite these the differentiated mesenchyme cells are seen.

Fig. 3. Syrian Bear. H. & E. (x 165)

Continuity of odontoblasts with matrix where not pulled away. Radiating tubules of predentine with empty appearance continuous with tissue fluid spaces, no suggestion of fibrils from the odontoblasts in tubules.

Fig. 4. Human. 4 months. (x 25 reduced.) Prof. E. B. Manley's section photographed by Mr. E. B. Brain.

Early development of dental epithelium showing connection of dental lamina with surface epithelium and extension for permanent tooth beyond enamel organ of milk tooth forming on the face adamantine. Around these marked proliferation of the mesenchyme cells with deeply stained nuclei. This most noticeable and constant collection of mesenchyme cells is called the "shower" by the author. Later some differentiate into pulp cells, odontoblasts and the supporting tissues of the teeth, see Diagram Text-fig. 1.

Fig. 5. Ring-tailed Lemur (adult). H. & E. (x 385)

Continuity of the tubules of dentine with intercellular spaces of the pulp and of the matrix with the odontoblasts. Capillary against palisade-like arrangement of odontoblasts at pulp surface. Curved tubules radiating from pulp suggest tissue fluid pressure during development.

Fig. 6. Brazilian Otter. H. & E. (x 165)

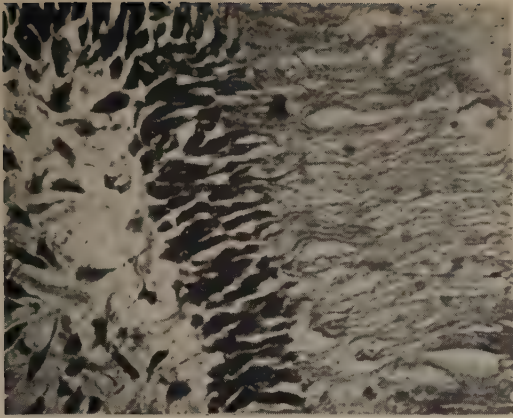
Wide predentine zone with collagen fibres from odontoblasts to matrix. Blood capillaries among odontoblasts. Tubules fine, numerous and continuous with interspaces of pulp.

Fig. 7. Amia. Azan. (x 165)

Odontoblasts continuous with matrix and tubules with intercellular spaces, evident but not well shown with the low power. The regularity of tissues is perhaps unusual. The superficial tissues have been displaced.

Fig. 8. Dogfish. Mallory. (x 385)

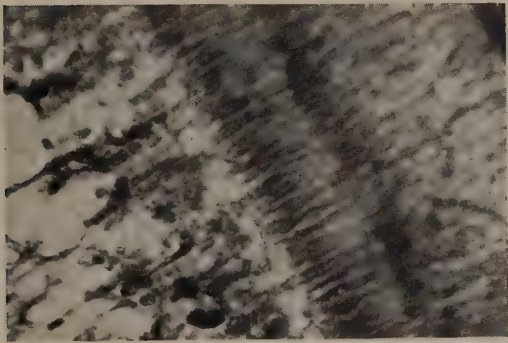
Developing dentine in an elasmobranch fish. Odontoblasts not in a layer as in mammals. Nucleus at round pulp end of cell, the opposite end conical and beyond the cytoplasm is continued as very long fibres to I.D.E. Complete formation of dentine occurs relatively at a later stage than in other orders. Relation of collagen fibres to cells is similar in all vertebrates. Appearance suggests atrophy of cells ceasing to function, seen as shadows. These long fibres grade to much shorter ones in mammals.



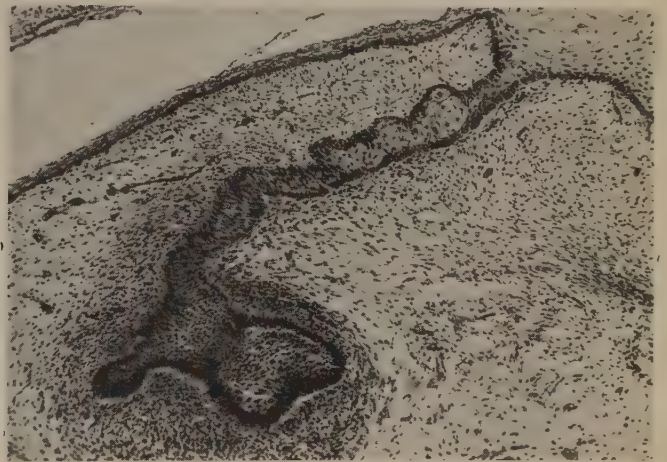
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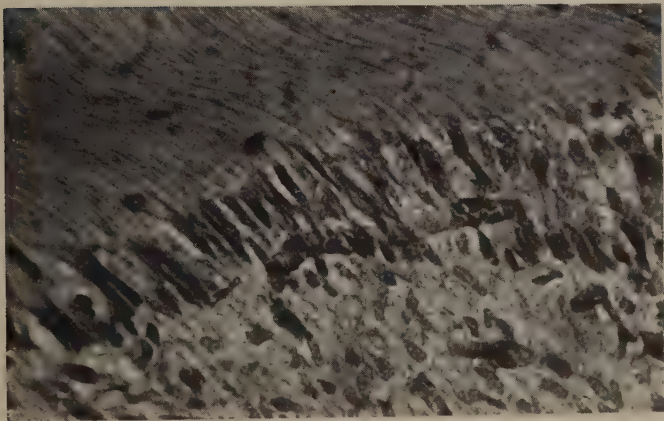
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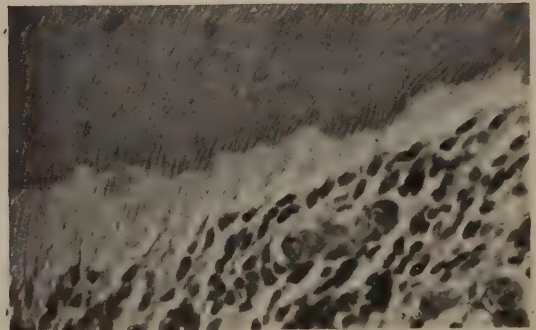
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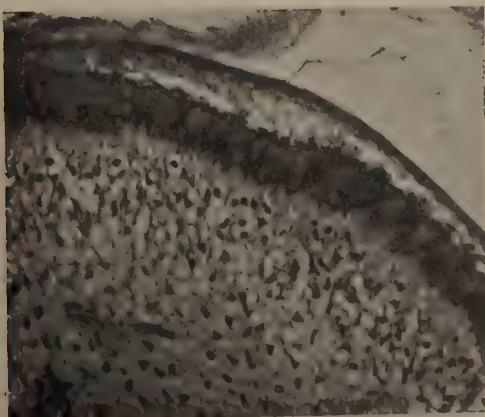
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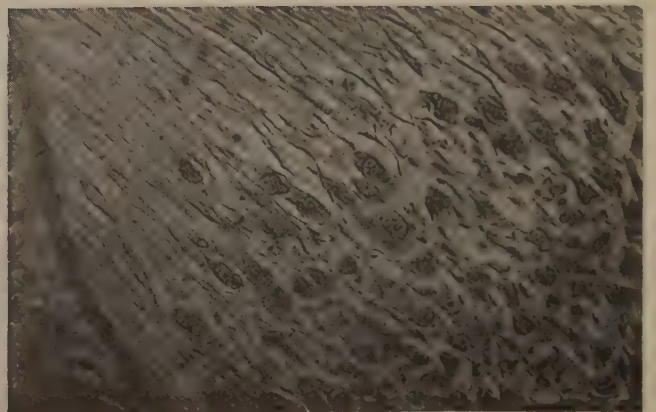
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PLATE 8

PLATE 8

A series of sections showing the relation of blood capillaries to the odontoblasts of the *Vaso-cellular barrier at the surface of the pulp*.

Fig. 1. Foetal Lion. H. & E. (x 90)

Relation of capillaries to pulp and odontoblasts, erythrocytes lost, endothelial cells distinct. Very fine branches among odontoblasts. The large number of capillaries in the pulp may explain the failure to demonstrate the finer ones in specimens injected under tension, pressure in the larger vessels compressing the finest capillaries. All the capillaries do not normally function at the same time, that some are always empty (Krogh, 1929) may be significant when injected.

Fig. 2. Brown Bear. H. & E. (x 385)

Section cut at Dental Research Department Birmingham University.
Blood capillaries and odontoblasts.

Fig. 3. Cod. H. & E. (x 385)

Long and narrow odontoblasts connected with matrix and numerous capillaries containing erythrocytes, the dentinal tubules unusually well shown for a fish.

Fig. 4. Cod. H. & E. (x approx. 1000). Same section as fig. 3.

Fibres passing from the ends and the sides of the odontoblasts to dentine matrix. Tubules and intercellular spaces continuous. Capillaries and odontoblasts closely related. Arrangement of tissues favours opinion that tissue fluid pressure radiates from the pulp during development.

Fig. 5. Iguana. H. & E. (x 385)

Developing dentine with bases of odontoblasts in close contact with vessels of the pulp which are so numerous that they occupy much of the pulp area in the region. The size of the erythrocytes with corresponding capillaries may account for them not being among the odontoblasts as in mammals. A pleurodont lizard, compare Pl. 3, fig. 5 for an acrodon.

Fig. 6. Puff Adder. H. & E. (x 385)

Numerous vessels in the pulp and against odontoblasts. Capillaries contain erythrocytes, those empty show endothelial cells. Similar to lizard, fig. 5.

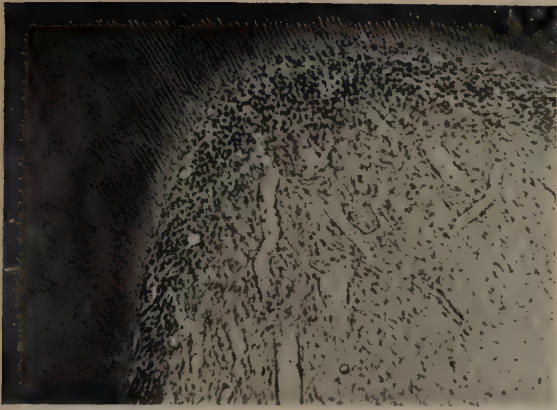
Fig. 7. Hamster. H. & E. (x 385).

Section cut Dental Research Department Birmingham University.

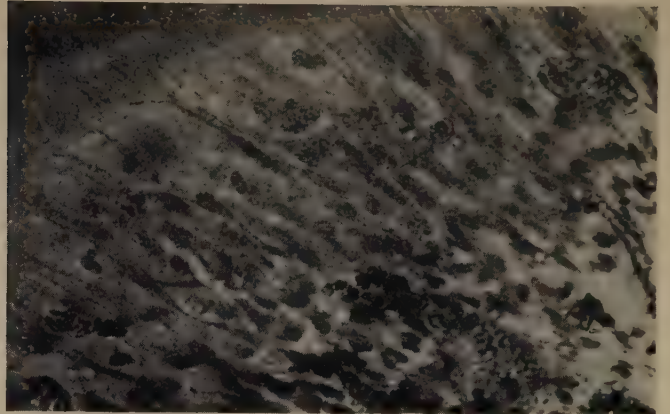
Relation of injected vessels to odontoblasts. Indian Ink injected into carotid artery of a living animal, the very fine capillaries have been penetrated to an unusual degree. The larger vessels of the pulp are alone more commonly seen in injected sections. An incisor with open base of persistently growing tooth and so probably freer blood supply of pulp when compared with a contracted apical foramen. Dr. Michaelson's injected specimen and also fig. 8.

Fig. 8. Kitten. H. & E. (x 165)

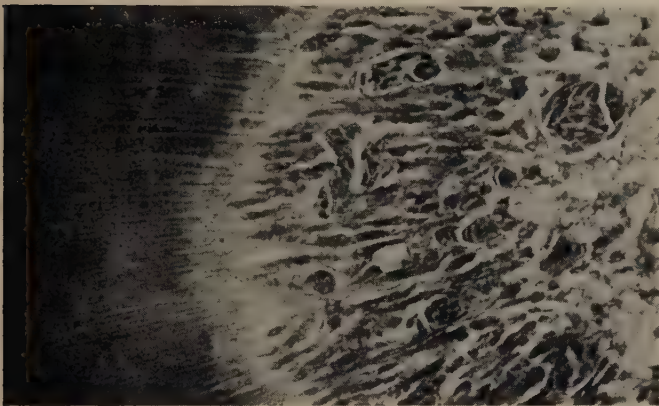
Vessels injected as in hamster, fig. 7, and fine capillaries reached. Surprisingly few are injected in the pulp, possibly due to lateral compression from the larger vessels, see caption fig. 1. In Pl. 4, fig. 4 from the same series of sections, the fine capillaries are not reached.



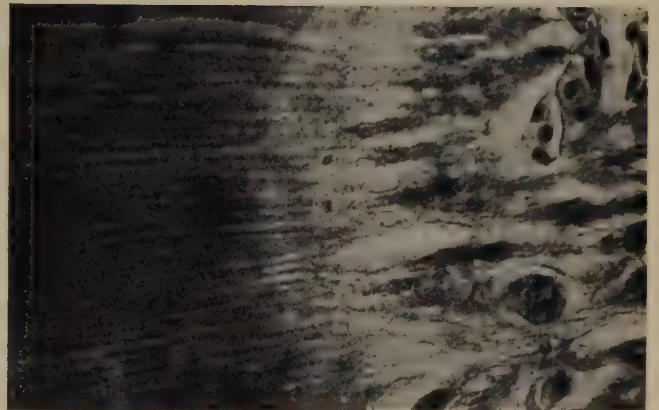
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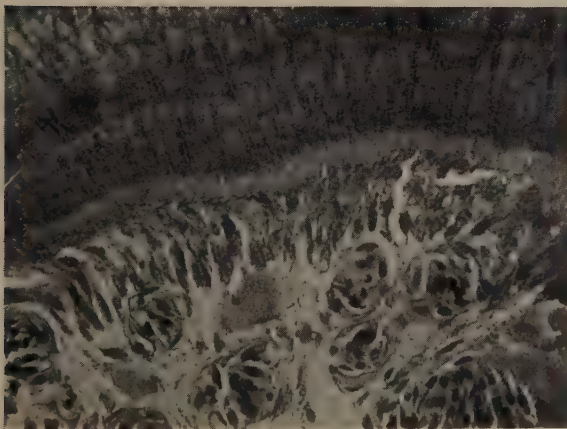
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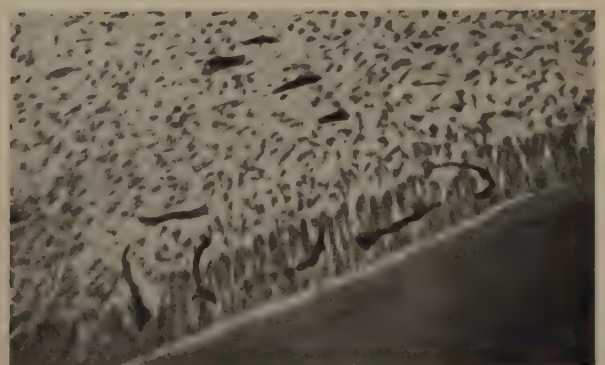
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PLATE 9

PLATE 9

Fig. 1. *Lepidosiren*. H. & E. (x 385)

Odontoblasts with deeply stained nuclei have associated fibres mostly running vertically into forming dentine. Fine tissue spaces are present between the fibrils without any dentinal tubules. The cytoplasm of the odontoblasts is indistinguishable from the forming fibres which are reticular and do not become collagenous is the probable explanation of this unusual appearance.

Fig. 2. Hake : *Merlucius merlucius*. (x 54) Photograph by Mr. Sawyers.

To demonstrate process of obliteration of channels pervading dentine. A ground section showing vaso-dentine. Vascular tubules present in the lower part of tooth are obliterated in the upper narrower part. Akin to the usual change in the tubules of mammalian teeth due to age or injury but not to same degree in non-mammals for their teeth are usually successional and of short duration. Occurrence of change in tooth of hake is extreme, channels are much larger than dentinal tubules so illustration of condition of "calcification" is more readily demonstrated. See fig. 3.

Fig. 3. Pigmy Shrew. H. & E. (approximately x 50) Photograph by Mr. Sawyers.

Tip of tooth fractured during life, secondary dentine formed and so called "calcification" of the tubules. Darker appearance of dentine matrix around the secondary dentine is an indication of change and similar to that seen at the worn surface dentine.

Fig. 4. Human : *Homo sapiens* (Incisor) (x approx. 1000) Bulk stain Carbol fuchsin.

Ground section, individual bundles of collagen fibres in the matrix. Intervening tubules and cementing substance not sharply defined although tissues not decalcified. Collagen fibres more compact nearer the pulp, suggesting diminished lateral tension in tissue fluid distally. An unusually thin ground section, the use of an oil immersion rarely gives so good a picture. Stain is hardly visible but defines the interglobular spaces which are near the surface of the dentine. Correlation of tubules and spaces imperfectly achieved. The spaces are flattened to thin irregular plaquettes.

Fig. 5. *Calamoichthys*. (low power) Dr. Easterbrooke's section.

Scale showing "dentinal tubules" at the surface of the scale beneath the surface epithelium pulled away. The layer below shows "canals" with vascular connective tissue from which the tubules radiate, the deepest layer the isopedine, not too well shown, is laminated parallel to the surface and contains some cells.

Fig. 6. *Protopterus*. Masson. (x 385) Dr. Easterbrooke's Section.

Large odontoblasts and developing dentine with indication of fibres, wide area of formed dentine which does not take the usual stains and probably the chief component being of the nature of reticular fibres, a condition characteristic of *Protopterus* and *Lepidosiren*.

Fig. 7. *Protopterus*. H. & E. (x 385)

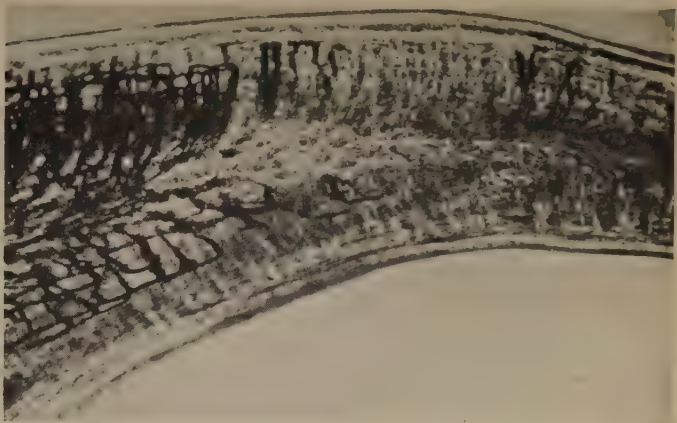
Forming dentine with "tissue spaces" but no indication of tubular arrangement. Fibres run in all directions, the most evident are parallel to the surface in formed tissue. Relation of the fibres to the cells is distinct, nuclei well shown, cytoplasm less evident.

Fig. 8. Bat. H. & E. (x approximately 1000)

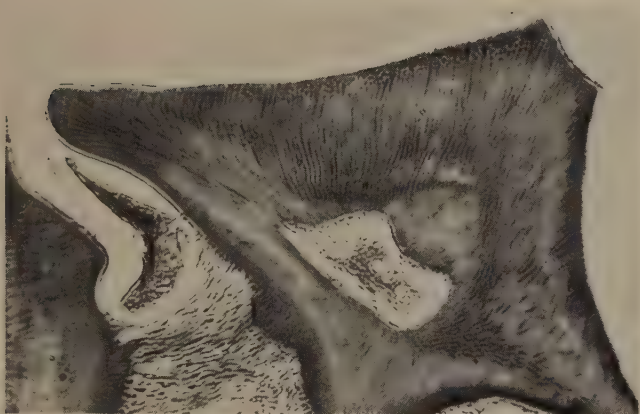
Fibres related to the odontoblasts pass into matrix of predentine, the dentine tubules continuous with spaces between bundles of fibres in pulp. Odontoblasts have large fusiform nuclei in long axis of tooth and ill-defined cytoplasm. Orientation of cells in tooth development is significant in constantly having their long axes parallel to that of the tooth, supporting the contention that radiating tissue fluid pressure is a factor in determining the conformation of tooth structures.



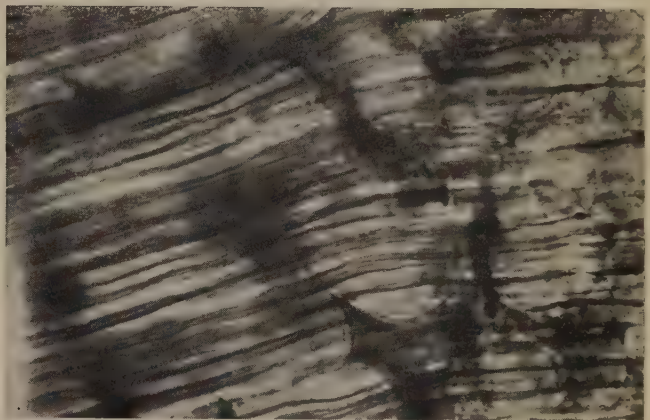
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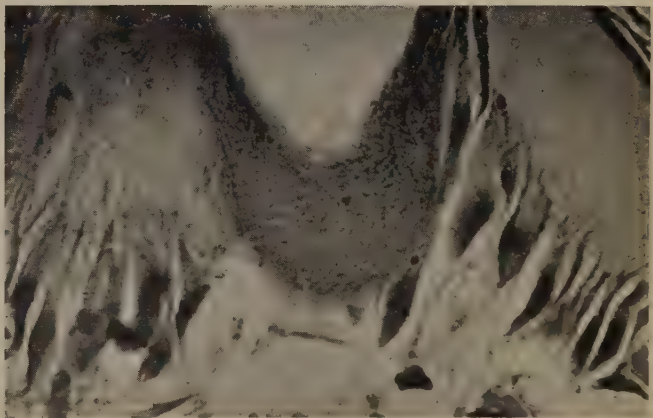
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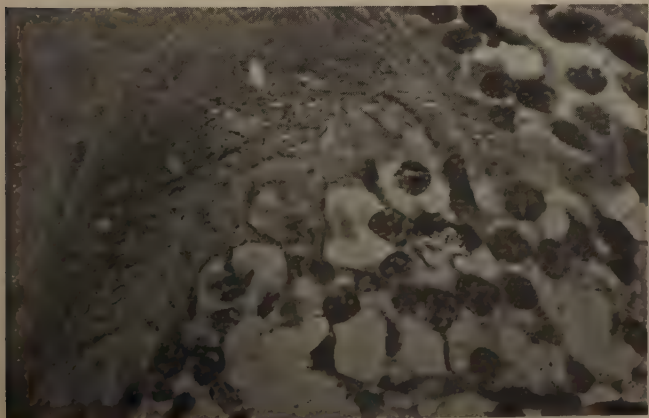
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PLATE 10

PLATE 10

Fig. 1. Human. Carbol fuchsin. (x 385) Prepared by Miss Agnew.

Ground section : wavy collagen bundles in dentine at pulp surface, dots and loops where cut across. Bulk staining the only prior preparation. Fibres with similar appearance are erroneously described as dentinal fibrils in prepared sections.

Fig. 2. Lamb. Robb Smith Silver Stain and Neutral Red. (x 165)

Developing dentine, very early stage. Bundles of reticular fibres laterally compressed appearance where more formed, vertical to basement membrane and I.D.E. layer of cells. Odontoblasts only just evident. The formalin fixative has emphasized bundle arrangement of fibres which are more developed passing from right to left where dentine formation is commencing.

Fig. 3. Python. H. & E. (x 385)

Longitudinal section of a tooth showing regularly spaced odontoblasts at side of pulp parallel to the forming collagen fibres also parallel to long axis of the tooth. Flattened arrangement of odontoblasts and forming collagen fibres is indicative of tissue fluid pressure.

Fig. 4. Lamb. Mallory. (x 385)

Early development of predentine. More magnified than in fig. 2, a little later and differently stained. The forming fibres upon the basement membrane are graded and are related to the odontoblasts. As in fig. 2 they are fine where first forming on the right, the more central are coarser, continuing to left are more developed to where dentine is just forming. Fixation with formalin emphasizes the bundles on account of the slight contraction.

Fig. 5. Mackerel. H. & E. (x 165)

Dentine of lateral walls with collagen fibres parallel to the long axis of the tooth and tissue fluid spaces between fibrous bundles of matrix. Odontoblasts not close to dentine but a layer of forming matrix with very wide tissue spaces corresponds with predentine. The arrangement of the tissues supports the view that pressure of tissue fluid is a factor in determining their positions.

Fig. 6. Cod. Silver stain (Lillie) (x 185)

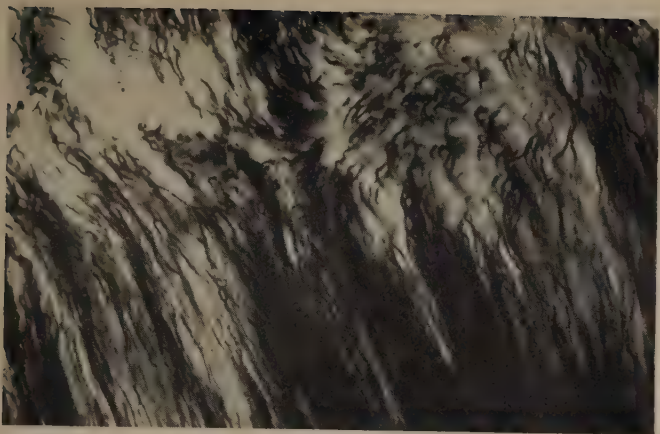
Reticular fibres at the margin of forming dentine. Fibres most distinct where further development of dentine will occur most rapidly. The outer aspect is suggestive of a continuity with a basement membrane.

Fig. 7. Minnow. H. & E. (x 385)

Side of root of developing tooth, odontoblasts vertical to forming dentine yet the collagen fibres run obliquely and become almost parallel to the long axis of the tooth wall, the fine channels or tissue fluid spaces lie between the collagen fibres of the dentine matrix. Arrangement attributed to tension of tissue fluids in the pulp.

Fig. 8. Dogfish. H. & E. (x 385)

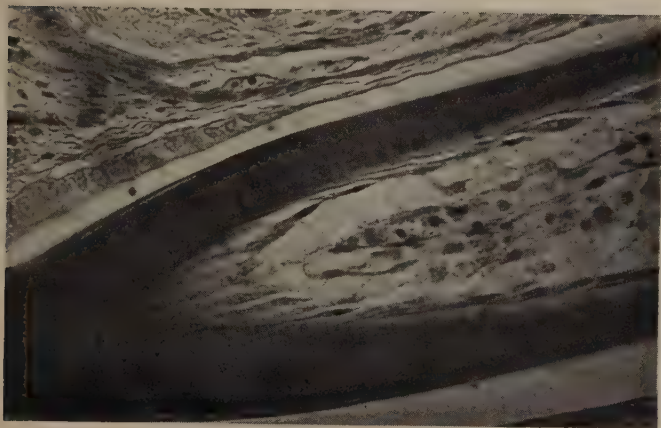
Early dentine development at summit of pulp. On the right I.D.E. cells cut in their long axis separated by basement membrane from collagen fibres. The thickness of the sharply defined basement membrane is due to a slightly oblique angle of sectioning. In contrast at the summit both are cut much more obliquely and show intermingling of fibres from the odontoblasts and the I.D.E. cells.



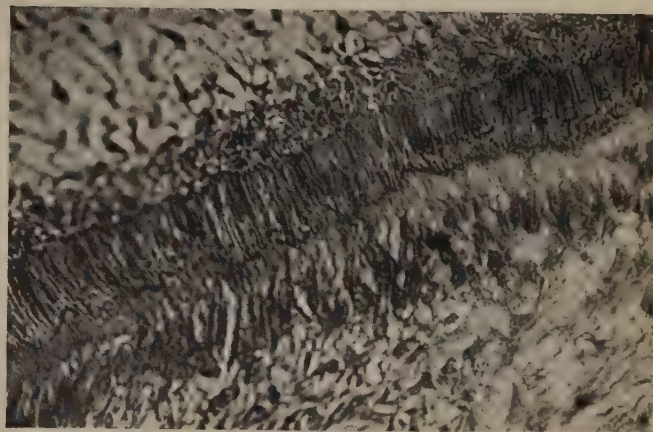
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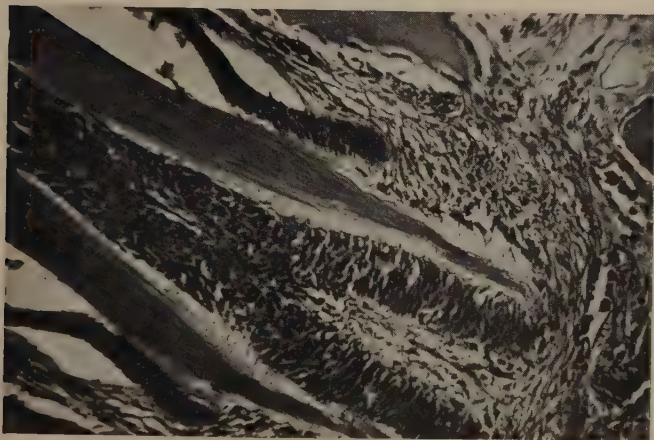
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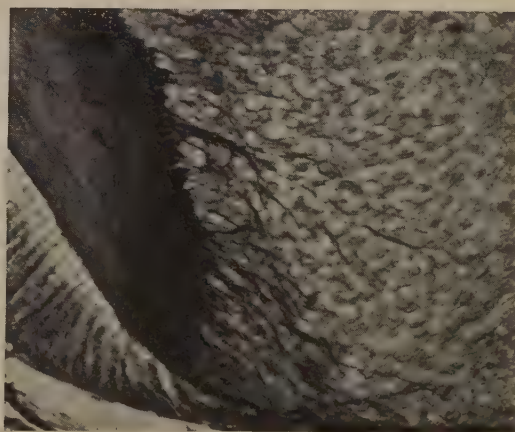
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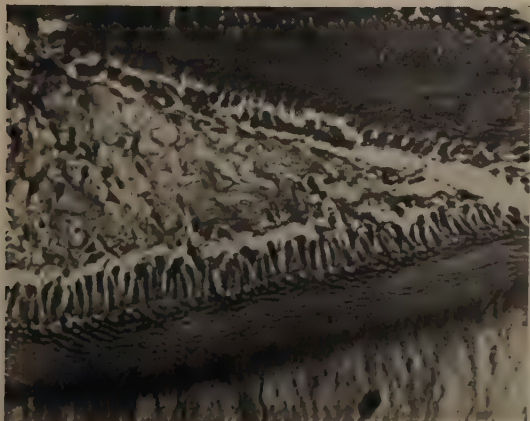
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Reproduction in the European Badger (*MELES MELES* L.)

By

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[Accepted 13th May 1958]

(With 5 plates and 5 figures in the text)

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INTRODUCTION

Reproduction in the European badger (*Meles meles* L.) has been the subject of controversy for many years. Naturalists both in Britain and on the Continent were very varied in their opinions both on the mating season and the period of gestation. Every month of the year has been claimed for the mating season by one authority or another (Fries, 1880 ; Cocks, 1903-4 ; Fischer, 1931 ; Notini, 1948 ; Neal, 1948 ; Harrison & Neal, 1956, 1958).

The general concensus of opinion on the Continent up to 1931 was that mating took place in the autumn or late summer, the period ranging between the extremes of July and November. Lönnberg (1928) favoured May as the likely month, his opinion being largely based on an account by Svantesson (1926) of mating observed in Sweden on May 27th 1926, and upon other less direct evidence. A similar diversity of opinion has existed in Britain, the evidence, as on the Continent, being fragmentary. Batten (1923) was strongly in favour of early spring as the most likely time. This opinion was based on much field observation, but he had not actually seen pairing take place.

Fischer (1931) studied the embryology of badgers in Germany and was the first to show that the badger exhibited the phenomenon of delayed implantation. He demonstrated that unimplanted blastocysts could be found from early January back to the previous July. His earliest date for finding blastocysts was July 30th, but as he had also a female with no blastocysts on August 6th in which follicles were present he assumed that mating took place during July or August.

Neal (1948) from observations in the field confirmed Fischer's embryological evidence by seeing copulation take place on four occasions between mid-July and the end of August, and further evidence was obtained by Pitt (1948) for mid-August. Notini (1948), however, showed that blastocysts were present in an unimplanted state in mid-May in Sweden. He also showed that ovulation could be stimulated by copulation in animals mated in captivity during May. Although embryological evidence pointed so strongly in favour of a spring mating, the significance of the July-September matings observed in the wild was obscure and there might have been a second ovulation. Ova liberated then might have been fertilized and might be those that subsequently implanted.

This paper is concerned with further investigations into reproduction in the badger (Harrison & Neal, 1956, 1958). Research was carried out along three lines: (a) intensive field observations over a number of years at all seasons. It was hoped that this would bring about a correlation between behaviour as noted in the field and the reproductive pattern as ascertained from histological changes in the genital tract, and at the same time provide a comprehensive picture of the reproductive biology of the badger, (b) limited embryological observations, (c) investigation of anatomical changes in the genital system.

MATERIALS AND METHODS

Over the course of ten years over seventy female and fourteen male badgers were examined. Some of these had been knocked over by cars, others had been killed by badger-diggers, keepers or pest-control officers. The great majority were from Somerset or Devon.

Each badger was weighed and its age roughly estimated using the categories "immature", "young adult", "adult", "old adult". The weight, condition of teeth and claws, weight of thymus and condition of the genital system and mammary glands were taken into account. (See Tables for details.)

The genital system was removed and dissected at once. Each uterine horn was carefully opened up and examined for unimplanted blastocysts. The contents were then washed out into a Petri dish with normal saline, and examined over black paper in case any blastocysts had been overlooked. Most of the material was then fixed in Bouin and later kept in 70 per cent alcohol.

Material from badgers killed after 1955 was also fixed in 10 per cent formalin, Rossman's fixative and chilled acetone. The majority of the ovaries were serially sectioned at 7 microns and stained with haematoxylin and eosin. Sections were also treated to demonstrate alkaline phosphatase by the method of Gomori (Dempsey & Deane, 1946). Other sections were stained by the periodic acid-Schiff technique of McManus (1946).

Observation on the animals in the wild was carried out by one of us (E. G. N.) and collaborators over a period of fourteen years. This included intensive watching from June 1943 to December 1945 at badger sets in Conigre Wood, Gloucester (215 visits including 104 at night) and more spasmodic watching in other localities in Gloucester and Wiltshire during the same period. Later observation at various times between 1941 and 1957 was carried out mainly in Somerset. Work was mainly concentrated, however, on a large community of badgers near Cushuish on the Quantock Hills over the years 1947-1955.

Keith Neal and Roger Avery kept up sustained and intensive watches from 1953 to 1957 both day and night at another set on the Quantocks. The behaviour of badgers at two different communities in the same district and under similar conditions could thus be compared.

Light was seldom sufficient for recognition of individuals and determination of sex, due to the crepuscular and nocturnal habits of badgers. This was overcome to a large extent by using powerful red torches to which the badgers paid no attention. Occasionally ordinary electric torches were used, but when used at ground level these were found to cause some uneasiness. Most observations were made from nearby trees 15 to 25 ft. from the set entrance to minimise diffusion of scent.

Further behaviour observations were obtained in collaboration with H. R. Hewer during 1951-1953, when young cubs and adult sows at Warminster, Wilts (1951-2) and Camberley, Surrey (1953) were habituated to strong artificial light over several months (March to June) and to the sound of a camera and eventually filmed.

THE CUB ; TIME OF BIRTH, CHARACTERISTICS AND BEHAVIOUR

Time of birth

No records are available of the exact dates on which badgers have been born in the wild because birth normally occurs in an underground chamber. Estimates of the dates have to be made from the following observations (a-d) :

(a) *The size of very young cubs.*

Records of observation of young cubs are given below :

When seen	Condition	Authority	Place	Estimated date of birth
Feb. 6	Just born	E. G. N.	Glos.	Early Feb.
Feb. 7	Eyes still shut	L. R. W. Loyd	Devon	Early Feb.
Feb. 10	About 10 days old	R. Murray	Devon	Early Feb.
Mar. 1	About 1 week old	E. G. N.	Somerset	3rd week Feb.
Mar. 17	About 3 weeks old	E. G. N.	Somerset	4th week Feb.
Mar. 27	About 3 weeks old	B. Nettleton	Yorks	Early Mar.
Apr. 14	3-4 weeks	R. Murray	Devon	3rd week Mar.
Apr. 19	5-6 weeks	R. Murray	Devon	Early Mar.
Apr. 20	3-4 weeks	R. Murray	Devon	Late Mar.
Apr. 22	5-6 weeks	R. Murray	Devon	Early Mar.

Of thirty-two cubs examined in Germany (Frank, 1940) it was estimated that the majority were born towards the end of February.

(b) *Cubs born in captivity.*

In Britain the following dates have been recorded for cubs born in captivity : February 13th, 16th, 27th and March 12th (Salvi, 1888).

(c) *First appearance of cubs.*

The following observations record the first appearance of cubs above ground and are correlated where possible with the behaviour of the sow at the estimated period of birth.

First appearance	Place	Authority	Estimated date of birth (taking into account size when seen)
16.3.53	Nr. Taunton	E. G. N.	Mid Jan.
28.3.57	Nr. Taunton	K. R. C. N.	Late Jan.
31.3.54	Nr. Taunton	E. G. N.	Late Jan.
1.4.55	Nr. Taunton	E. G. N.	Late Jan.
1.4.56	Nr. Taunton	E. G. N.	Late Jan.
4.4.57	Nr. Taunton	R. A. A.	Early Feb.
5.4.44	Rendcomb, Glos.	E. G. N.	Early Feb.
6.4.55	Nr. Taunton	E. G. N.	Early Feb.
15.4.56	Nr. Taunton	R. A. A.	Early Feb.
11.4.45	Rendcomb, Glos.	E. G. N.	Early Feb.
11.4.55	Nr. Taunton	K. R. C. N.	Early Feb.
13.4.54	Nr. Taunton	K. R. C. N.	Early Feb.
25.4.56	Nr. Taunton	K. R. C. N.	Mid Feb.
17.4.45	Warminster	E. G. N.	Mid Feb.
Mid April 43	Rendcomb, Glos.	E. G. N.	Mid Feb.
Mid April 54	Nr. Taunton	E. G. N.	Mid Feb.
20.4.53	Camberley, Surrey	E. G. N.	Mid Feb.
28.4.46	Rendcomb, Glos.	E. G. N.	Late Feb.
29.4.56	Nr. Taunton	E. G. N.	Late Feb.
1.5.45	Rendcomb, Glos.	E. G. N.	Early Mar.
12.5.54	Nr. Taunton	K. R. C. N.	Mid Mar.

(d) *Embryo size.*

The C.R. length of embryos recovered from animals killed in south-west England is given in Table 10, p. 103. The estimated date of birth for all but one lies between late January and early February.

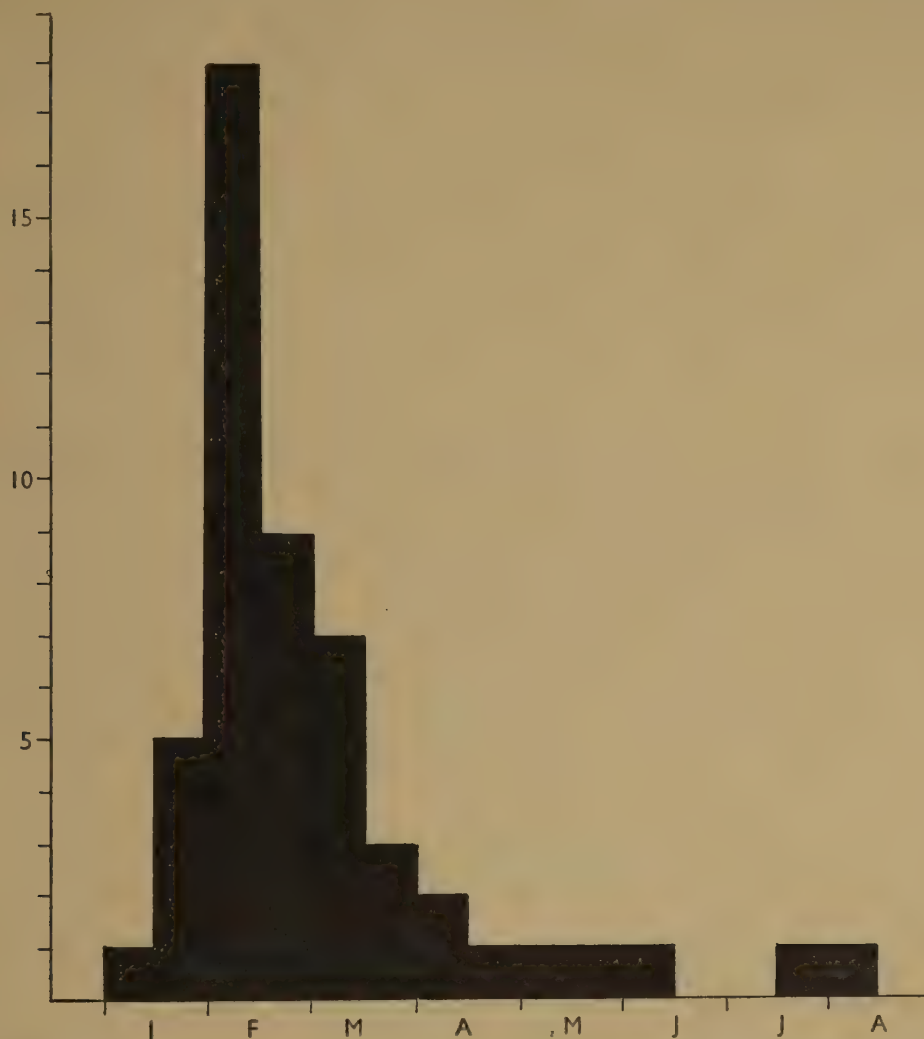


Fig. 1. Frequency distribution of estimated times of birth of litters in south-west England (January to August): see observations (a-d) pp. 70-71.

Fischer (1931) records embryos of 3 mm. on January 2nd to 100 mm. on February 3rd. Notini (1948) observed embryos of 4-5 mm. on January 7th to 103 mm. on February 10th. Unusually late dates have been recorded. A cub with eyes still shut was found in early June in Germany (Frank 1940). A sow knocked over by a car in Somerset was still suckling (August 4th): this was probably a May birth. The latest records are from Devon, where two families, each of three cubs, were dug out on July 29th and August 5th 1956, their age

being estimated at three to four weeks. (R. R. Murray, private communication). Thus it would appear that births as late as July are possible.

It can be concluded that the time of birth in south and south-west England is most frequently during the first three weeks of February. Births during the latter half of January are not unusual in milder parts. March births are frequent, but births after mid-April are exceptional. Further north, late February and early March are the peak periods as in Germany. In Sweden early March is the usual time (Notini, 1948), in southern France births in January are common (Canivene & Laffargue, 1956).

The number of cubs

Litter size from the numbers of foetuses and newborn cubs is given below :

	Total litters	Singles	Twins	Triplets	Quads	Average
<i>England</i> (E. G. N.)	10	1	0	6	3	3.1
<i>Germany</i> (Fischer)	7	0	2	5	0	2.7
<i>Sweden</i> (Notini)	34	4	13	14	3	2.47

Numbers in a litter may be recorded from observations of cubs when above ground about eight weeks after birth. The following litter numbers have been recorded in south-west England (1939-56) : singles, 9 ; twins, 23 ; triplets, 11 ; quads., 7. Total : 116 cubs from 50 pregnancies ; average litter size, 2.3. Cowen (1955) gives a similar frequency sequence. There is one authentic record of a litter of five (Nettleton, 1957), and a number of other families of five have been seen above ground. Two families may live together, so it is doubtful if these are reliable observations. As many as five unimplanted blastocysts have been seen on several occasions in the uterus, but it does not follow that all these would have implanted.

Infant mortality

Although numbers taken are rather small, there is a significant difference between the number of embryos and the number of young at eight weeks. This amounts to a loss of nearly 26 per cent in our series. Dead cubs (aged six to seven weeks) have been found outside the set on several occasions. A small cub with its viscera eaten out was also found outside a set, but it is not clear what had killed it. There are several records of dogs having brought out young cubs during the day. The mother is not always in the nest chamber with her cubs at this time because normally she would defend her cubs from a terrier without difficulty.

Nesting chamber

Evidence obtained at Rendcomb, Glos. (Neal, 1948) showed that not every badger set was used for breeding purposes. Each had to be enlarged sufficiently over two or three years to have several chambers, and usually more than one entrance, before breeding took place.

The breeding chamber is usually an enlargement of a side tunnel. It is $1\frac{1}{2}$ to 2 ft. high with a diameter of 2 to 3 ft ; it may have a second tunnel leading from it. Evidence from badger diggers suggests that it is often not far from the entrance. During the winter on a frosty morning water vapour was rising like steam from the nearest entrance of a set at Camberley due to heat from the badgers' bodies. Bedding used for the cubs was taken down the same hole and later the cubs were heard being suckled approximately 4 to 5 yds. in. Good ventilation may be an important factor in choice of situation and distance from an entrance. Evidence of the position of the chamber in relation to the nearest hole is obtained by watching for signs of bedding being brought in during the period January–March.

The breeding chamber is full of bedding consisting of dead bracken, hay, leaves, moss and other material. The young cubs are buried in this litter and when very small the mother with them. The mother may leave them for a time later on.

The temperature of the nesting chamber when the cubs are born is believed to be quite high, an important factor for survival. The bedding acts as insulation and the mother's body supplies heat.

A maximum/minimum thermometer on the end of a long springy wire was pushed into a set as far as possible, left for a while, and withdrawn. Cold weather was chosen before the cubs were born. It is not known if the thermometer reached the nesting chamber, but it is unlikely that it did. On January 12th 1956 at Cushuish, Somerset, set A had two entrances. Air temperature outside was 40° F., up to 10 ft. within the entrance it was 44° F.—a rise of only 4° F. On February 2nd snow covered the ground. The upper entrance showed snow melting round the hole although there was no sun on it. The lower entrance was frozen. A warm current of air could be felt coming out of the top entrance. The temperature outside was 20° F., in the entrance it rose 5° F. ; 4 ft. 9 in. in the temperature rose to 32° F., and 6 to 8 ft. in to 34° F.—a rise of 14° F. Similar experiments at another set on the corresponding days showed only a rise of $5\frac{1}{2}^{\circ}$ F. on January 12th and 7° F. on February 2nd, suggesting that the thermometer either did not get near the nesting chamber or that there was not one at that set.

Breeding rarely takes place above ground, but it has been observed in Somerset. The country was flat, liable to flooding, and the peat too loose for digging : this probably explained the breeding nest being above ground. The nest was in a hedgerow of hawthorn and consisted of a large mound of dry hay about 3 ft. high and 4 ft. in diameter at the base. On poking the pile (1.3.56) a sow badger jumped out of the top of the nest and three small cubs about a week old were found buried deep down. The disturbance caused the sow to move her cubs the following night to a safer place.

Description of the cub

Foetuses 120 mm. in length have been found with hair, and Lönnberg (1928) describes a newly born cub of the same length. This is the usual birth size. The fur is usually dirty white, and facial stripes can sometimes be seen after a few

days. A cub aged about twenty-one days was 24 cm. long, including the tail (7 cm.); the general colour was grey with a brownish tinge on the head. Individual hairs were uniformly grey but some had a short white base. No facial stripes were visible. The eyes were open, the ears relatively large and the primary dentition was erupting.

The eyelids are fused at birth: most evidence suggests that the eyes open ten days later. Hiller (1926) describes three cubs found on January 19th, two with eyes closed and one just open. As this is one of the earliest births recorded it is unlikely that the "blind" period could have been more than ten days. There is some confusion in the literature between "eyes open" and "able to see". Observations on tame badger cubs suggest that they are virtually "blind" for as long as four or five weeks in the sense that they cannot focus adequately on near objects. In the wild they would be living during this period in complete darkness.

Growth rate

Cubs born in the wild in February appear to be nearly as big as small adult sows by the autumn, but their growth rate varies according to the available food and hence weather conditions. During the dry summer of 1955 cubs were smaller than usual by the autumn and could be distinguished from adults up to the following spring. This could be correlated with lack of earthworms due to dryness and lack of rabbits due to myxomatosis.

Weighings of dead badgers up to sixteen months old give a general picture of growth rate under wild conditions in south-west England.

Date	Females	Males	Calculated age
14.6.47	7 lbs	9 lbs	4- 4½ months
5.8.54	—	14 lbs	6 months
25.8.53	15 lbs	—	6- 7 months
15.10.55	—	21 lbs	8 months
19.12.54	24 lbs	—	10 months
21.1.50	20 lbs	—	11-12 months
15.2.52	14 lbs	—	12 months
24.2.54	16 lbs	—	12 months
30.4.55	15½ lbs	—	14½ months
30.4.55	16 lbs	—	14½ months
1.5.49	18 lbs	—	15 months
5.5.48	14 lbs	—	15 months
10.5.53	18 lbs	—	15 months
2.6.54	15 lbs	—	16 months

The drop in weights after January is characteristic of both cubs and adults and suggests utilization of fat. Animals killed on January 21st 1950 and December 19th 1954 were very fat indeed. No large fat deposits were present in animals killed after the end of February. Records for captive badgers show

the same tendencies, but the growth rate is faster. Frank (1940) gives the following figures for a male and a female cub brought up in captivity :

	Male	Female
May 1	3 lbs 10 ozs	5 lbs 4 ozs
June 1	5 lbs 4 ozs	8 lbs 4 ozs
July 1	12 lbs 8 ozs	14 lbs 0 ozs
Aug. 1	20 lbs 0 ozs	18 lbs 0 ozs
Sept. 1	26 lbs 0 ozs	21 lbs 0 ozs
Oct. 1	29 lbs 0 ozs	27 lbs 0 ozs
Nov. 1	31 lbs 0 ozs	30 lbs 0 ozs
Dec. 1	34 lbs 0 ozs	29 lbs 0 ozs
Jan. 1	37 lbs 0 ozs	27 lbs 0 ozs

The male tends to be heavier than the female and the latter shows a drop in weight from November onwards.

Cub behaviour

Early appearances above ground.

First appearances of the cub above ground usually occur about eight weeks after birth. After six weeks the cubs are old enough to start exploring the underground tunnels and by seven or eight weeks may come to the entrance. The earliest date cubs have been seen at an entrance was on March 16th 1953 on the Quantocks soon after dark on a dry frosty evening.

Continuous watching for ten nights at Camberley between April 18–28th 1953 gave a good picture of early behaviour. Cubs were first seen on April 25th, although previously their shufflings and wickerings had been heard down the tunnel. Two cubs appeared at the entrance at 10.50 p.m. in close contact with each other. They were constantly on the move, investigating each stick or leaf within reach and testing out their sense of balance on the sloping sides of the entrance. They were visible for about ten minutes on this first occasion. They appeared again at 1.35 a.m. and were out for rather longer. The next evening they were seen at 8.40 for a short time and again at 1.0 a.m. for twenty-five minutes. On each of these occasions the sow was below ground but near the entrance, and at times her low purring could be heard which was taken to be a means of giving confidence to the cubs.

When only one cub is present behaviour is somewhat different and the sow brings the cub out. On April 28th 1946 a cub kept to the entrance with its mother until she got up. It then followed her and crept under her body. The sow then walked slowly forward with the cub almost hidden by her body. After a few yards the cub came out and scampered back to the set.

The appearance of the cubs above ground when nine weeks old becomes more regular. They normally appear before it is dark and their activity becomes more pronounced. Their powers of co-ordination increase and their play consequently becomes more variable and purposeful. At this stage they will tumble each other over and bite at ears or tail.

Associations are quickly built up in relation to the senses of scent, touch and hearing. Early on, any sudden noise results in a scamper for home ; later they

learn to discriminate between sounds and are not disturbed by familiar harmless noises. Very few visual associations are built up for ten or twelve weeks, the main reaction being one of fright when any pronounced movement is seen.

The cubs become more venturesome when ten to eleven weeks old and contact assurance is of less importance. They will explore the near environs of the set and play becomes violent and prolonged. As a result the ground outside the entrance is beaten flat and hard and little vegetation remains.

By twelve weeks the cubs extend their explorations for some distance round the set. They start searching for food, but they are still dependent upon the mother. Weaning starts at this stage, regurgitated food being substituted for milk (Notini, 1948). By fourteen weeks weaning has finished and the cubs are away from the set for many hours searching independently for food, but being within hearing distance of each other most of the time. The sow often goes off on her own.

Play is most pronounced when twelve to fourteen weeks old—a time before the quest for food becomes a major activity. The cubs will often emerge in good light and play for long periods while the sow is away. After periods of play the cubs will start to forage and move slowly away from the set. Certain patterns of play are also detectable (Neal, 1950). When families are large or when two litters are living together play is more pronounced. A single cub plays to some extent with the sow, but foraging soon becomes more important than play.

A number of adult activities are foreshadowed during development. Setting scent on objects near the set occurs early, although it is often difficult to observe in the wild owing to the low position of the body. Tame badger cubs show this to a remarkable extent. They start making snuffle holes with snout and claws in their search for food, and by July trial sets are dug out which may not go in more than a foot or so before being abandoned.

Shuffling backwards with leaves and sticks is often observed from nine weeks onwards. At first, only momentary, it later becomes sustained and develops into the habit of bringing back bedding to the set. Observations on tame cubs by Nettleton show that although never being in contact with other badgers after ten days old they, nevertheless, carry out all these actions in a similar way, suggesting that setting scent, forming snuffle holes, digging and bringing back bedding are basically instinctive and not learned.

Movements of cubs

Variations in the number of adults and cubs at certain sets have been studied over several years. Some cubs leave the parental sets in autumn or winter; in 1945 there was a drop in numbers in the Rendcomb sets in October. This also occurred the following year at the same set at the same time and corresponded to the digging and occupying of holes a mile away in which no cubs were born the following spring. In 1954, near Taunton, there were four adults and five cubs in a wood during the summer. By mid-December there was a boar and sow at one group of holes, another boar and sow at a second, and the cubs were in others. The same picture was true of the three previous years. At another set

a drop in numbers occurred in November 1954 but some cubs were still present by the end of the month. By early December only adults were present. In 1955 a male cub had left by September 7th, but the remaining two female cubs stayed all the winter. At Yeovil in 1951 (Vaughan, private communication) all six cubs from two families had left by October 17th.

These observations suggest that the parents remain in breeding sets to breed another year while cubs usually move off. Badger diggers usually find immature animals in the outliers or smaller sets after December. In large sets, however, some cubs, more often females, undoubtedly remain until the following spring.

SEXUAL MATURITY AND TIME OF MATING

Sexual maturity

Notini (1948) states that badgers become sexually mature when two years old. In Britain most female cubs become sexually mature when twelve to fifteen months old (see p. 93). On December 26th 1945, a cub aged about ten months was marked on her ear; the parents were killed. She was caught again at the same set on June 16th 1947, this time with two cubs aged about four months. Thus the mother was born in early spring 1945, mated in 1946 and had cubs in 1947. A female cub reared by one of the wardens of the Wildfowl Trust, at Slimbridge, Glos., came on heat the following February when approximately twelve months old. H. G. Hurrell (private communication) had cubs attempting to mate in February at twelve months old.

Seven immature females (Table 2, p. 92) were obtained between January and May. Judged by weight, condition of teeth and thymus size they were considered to be between ten and fifteen months old. Animals B.7-13 and B.16 (December-February) showed signs of approaching oestrus and had follicles 2 mm. in diameter in the ovaries. Animal B.14 (5.5.48) was late in becoming mature and had follicles of only 0.5 mm. in diameter. This suggests that maturity late in the second year is also possible.

Limited work carried out on male cubs, both in the field and in captivity, indicated that they may not be mature until two years old.

Time of mating

One authority or another has made claims for each month of the year as the mating period. This diversity of opinion is summarized by Notini (1948) and Neal (1948).

Observed pairings

It was generally believed before 1860 that mating took place in the autumn. Records published in "The Field" (1860-67), summarized by Cocks (1903-4), showed a number of unusually long gestations that would be incompatible with an autumn mating. Animals captured during spring and summer and subsequently isolated gave birth to cubs the following spring. Paterson (1904) observed captive badgers attempting to mate on July 10th, 1898; they copulated successfully two nights afterwards. Lönnberg (1928) quotes Svantessen as having observed mating in the wild in Sweden in May. Neal (1948) observed

mating in the wild on July 14th, 29th and 30th, and an attempt at mating on August 25th. Many more observations of mating at different times of the year have now been made. The results of these personal communications and of observations by one of us (E. G. N.) are given below.

Date	Authority	Place	Remarks
Feb. 5 1925	Hurrell, H. G.	Devon	Captive badgers born the previous year. Attempt only.
Feb. 10 1957	McDermott, C.	Kent	75 mins. duration.
Feb. 12 1957	Neal, K. R. C.	Somerset	1 min. duration.
Mar. 16 1955	Neal, K. R. C.	Somerset	10 secs. duration. Attempt only.
Mar. 20 1951	Vaughan	Somerset	10-15 secs. duration.
April 1 1952	Howard R. W.	Dorset	2 mins. duration.
April 2 1952	Vaughan	Somerset	15 mins. duration.
April 4 1952	Howard, R. W.	Dorset	On and off for several hours.
April 5 1952	Howard, R. W.	Dorset	Same badgers on and off for more than 1 hour.
April (end of 1952)	Stansfeld, Col.	Wilts.	15-20 secs. duration.
May 9 1953	Elliott	Yorks.	15 mins. duration.
May 27 1926	Svantessen	Sweden	Duration not given.
July 10 1898	Paterson	England	Captive badgers. Attempts only.
July 12 1898	Paterson	England	Certain mating. Duration not given.
July 14 1945	Neal, E. G.	Glos.	Duration less than 1 min.
July 21 1945	Grant, Hill and North	Glos.	Duration less than 1 min.
July 27 1952	Wild	Kent	Short duration.
July 27 1952	Lancum, H. W.	Devon	About 40 secs.
July 29 1945	Neal, E. G.	Glos.	Duration less than 1 min.
July 30 1914	Loyd	Devon	Duration not given.
July 30 1919	Loyd	Devon	Duration not given.
July (last week of)	Wild	Kent	Short duration.
July ?	Platt, H.	Salop	Two cases of short duration.
Aug. 13 1943	Pitt, F.	Salop	Short duration.
Aug. 20 1952	Lancum, H. W.	Devon	Attempt only.
Aug. 25 1945	Neal, E. G.	Glos.	Attempt only.
Aug. 30 1951	Howard, R. W.	Dorset	Short duration.
Sept. 2 1951	Howard, R. W.	Dorset	Short duration.
Sept. 5 1946	Blackmore, M.	Devon	Short duration.
Sept. 24 1951	Howard, R. W.	Dorset	70 mins. duration.
Oct. 8 1955	Avery, R. A.	Somerset	Attempts only.

Several points should be borne in mind when assessing the value of these observations.

1. Far more badger watching has been done between April and September than during the rest of the year. Intensive watches were planned for February and March over three years, but long periods of frost and snow and other factors unfortunately limited observation. However, at one badger community fifteen watches were made in January, ten in February, twenty-eight in March over the years 1954-6 (K. R. C. N. and R. A. A.) and others were made elsewhere.

2. It is normally only possible to watch badgers for long periods near their sets and mating may take place out of sight. Judging by the vocal noises known to be associated with pairing, especially the deep "purring" of the boar and the general excitement, this may well have happened just out of sight on three or four occasions between February and April.

3. Most watching was carried out between dusk and midnight, far less towards dawn. This is not important as on almost every occasion the sow was mounted immediately on emergence. No sign of pairing has been observed when badgers return towards dawn.

4. Pairing may take place below ground and thus escapes observation. It is not known whether this happens but it seems unlikely judging by the size of the tunnels and chambers and the fact that Howard (private communication) once observed the sow being dragged out by the boar before being mounted.

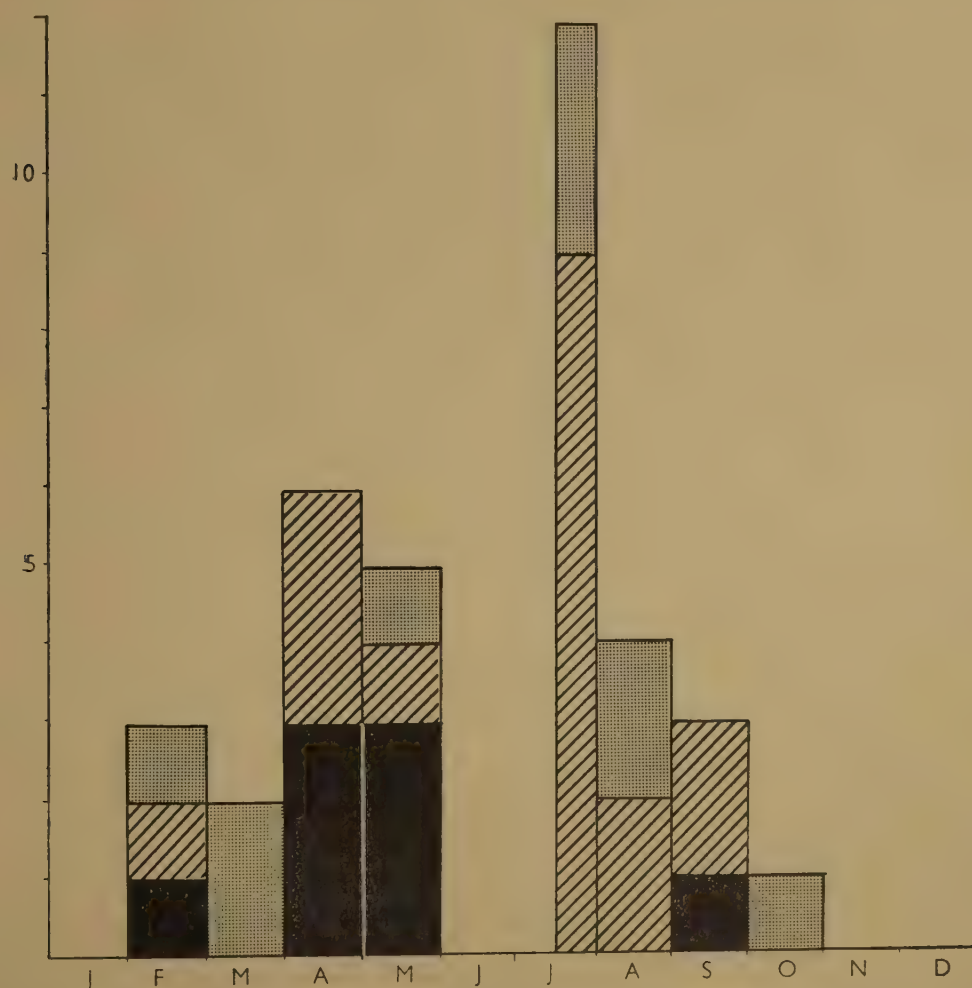


Fig. 2. Frequency distribution of observed pairings in badgers in south-west England (January to December) *Black squares*=long duration pairings, more than 15 mins. *Diagonal hatching*=short duration pairings, less than two minutes. *Dots*=attempts only.

Observational data *only* suggests that copulation can occur in southern England in each month between February and October with a possible gap of about two months between mid-May and mid-July. There are, however, certain aspects of behaviour during mating which appear to be important.

The duration of copulation observed is very variable. The greatest number have been of two minutes duration or less, but there have been others of fifteen minutes. Howard on three occasions has observed mating for more than an hour (on April 4th and 5th and September 24th) and McDermott for seventy-five minutes (February 10th). It is well known that other members of the Mustelidae pair for long periods, e.g. *Mustela vison* (thirty to forty minutes), *Martes zibellina* (fifty minutes), *Mustela furo* (up to three hours) (Asdell 1946). The question arises whether the short duration pairings are effective in bringing about fertilization ; this is discussed on p. 115.

Excitement between adult boars and sow badgers is likely to be correlated with their sexual activity, and the dates when this has been observed have always been noted. Extensive watching between 1944-56 showed that excitement is greatest during the period February-April, but that throughout the period May-October occasional nights of considerable excitement occur separated by long periods of normal adult behaviour. Excitement includes violent play and scuffles, much vocal expression (especially deep purring by the boar), raising of the tail and fluffing out of the fur, and emission of scent from musk glands. This pattern of behaviour was also observed by Vaughan (private communication) who writes : "The period of excited play took place (Yeovil) from the second week of February, was at a maximum during the middle of March and then decreased to ordinary movement in early May. From then on there was little excitement".

MATING BEHAVIOUR

Observed pairing is of two kinds, i.e. of short or long duration. The latter only occurs when the sow is in full oestrus, but for reasons to be discussed later the sow will receive the boar at other times.

Short duration pairings have now been described on nineteen occasions. Four were recounted by Neal (1948). On some occasions there was no preliminary play of any kind. On others there was considerable excitement with violent play and much emission of scent from musk glands. Sometimes the female received the male quite passively ; at other times she refused at first by flattening her body on the ground. On no occasion was the sow really excited or appeared to invite the boar.

Mounting was often preceded by much purring by the boar. This is a deep vibrant noise and is a most characteristic feature of sexual excitement. The first sign of interest shown by the boar is often the raising of his tail into a vertical position. The boar may then approach with a shuffling motion making a series of short steps with the legs kept rather rigid. On mounting dog-fashion, the male grasps the female with his front legs in front of her flanks. He keeps his position by gripping her neck or ear with his teeth, sometimes waving his head

from side to side before getting another grip. He keeps in this position for a length of time ranging from about fifteen seconds to two or three minutes.

Short duration pairing has been observed both when cubs have been present and when adults have been living alone.

With long duration pairings, ranging from fifteen minutes to several hours, a similar general plan of behaviour is exhibited but with greater intensity. There is great excitement among the male population and considerable rivalry is apparent if several males are present. Once the sow appears, purring is almost continuous—it sometimes rises to a much higher note reminiscent of a prolonged whistling neigh (when the dominant boar has heard a rival in the vicinity). The sow occasionally makes a high-pitched staccato note like that of a moorhen. The raising of the tail is also most obvious on these occasions. This may be initiated by the sow when she is in full oestrus (Howard, 1956), but more often it first takes place in the boar. On several occasions the boar was observed prior to pairing to turn his back on the sow, raise his tail and back on to her. This action is almost certainly concerned with setting scent. Badgers will commonly set scent on objects in the vicinity of the set and when travelling in unfamiliar country. The former may be of territorial significance, but when it occurs prior to copulation it would appear to be as a sign of possession. Howard noticed it particularly when a rival boar approached the sow. When the boar approaches the sow and purrs it often stretches its neck forwards and slightly lowers its head. The sow on the other hand if it desires attention will swing round on the male, lower her head and raise her hind quarters (Elliott, personal communication).

Howard (1956) watched at a set in Dorset on the nights of April 1st to 6th; there were two boars and one sow. On April 1st he saw two badgers pair for about two minutes. On April 4th and 5th copulation was observed on and off for several hours. On April 6th all sign of sexual activity had abated. It is probable that the sow was coming into oestrus on April 1st, was in full oestrus on April 4th and 5th, and that this oestrus only lasted for a few days.

On April 4th and 5th both boars copulated with the same sow during the evening, showing that badgers can be promiscuous under certain circumstances. Much circumstantial corroboration of this was obtained by population studies over three years at two sets on the Quantocks. On several occasions, usually for short periods, there was a marked increase in the number of boars at a particular community, accompanied by a general increase in excitement.

Observations at smaller sets suggest that badgers are not always promiscuous. Howard saw copulation on September 24th when only one male and one female were seen although the sow was apparently on heat and pairing lasted for at least seventy minutes. Elliott's account (1955) of pairing at a set near Sheffield on May 9th told of only a single pair, and the same applied to pairing on February 10th witnessed by McDermott in Kent.

On nights when sexual excitement, especially in the boar, is considerable, violent play or attempts at mating may suddenly be interrupted by a bout of violent digging or the bringing back of a bundle of bedding towards the entrance, only to be abandoned. This might be courtship behaviour or merely displacement

activity. The latter is more probable in the case quoted from Howard's observations when a boar not in possession began to dig small pits in the vicinity while another boar was pairing.

VARIATIONS IN ADULT BEHAVIOUR

Variation in sexual behaviour from one year to another

Regular watching over a number of years at certain sets shows that there is much variation in the amount of excitement and that periods of excitement may not correspond exactly in successive years. Sometimes April has been marked by inactivity with very little excitement; in other years it has been full of incident. Bouts of excitement in May over a few nights one year have been followed the next year by more uniform behaviour.

There are several factors which may have a bearing on this:

1. The date of birth of cubs varies from one year to another and consequently the date of the sow's first oestrus may vary accordingly. This may affect the date when other boars visit the set and sexual excitement becomes evident.
2. Cubs of the previous year sometimes leave the parental set in the autumn, but they may remain as late as May of their second year. The female cubs may become mature from February onwards. This will influence the number and behaviour of the male population.
3. The number of families living in the one community varies at any one time from one to three. The more there are, the more likely excitement will be observed.

Formerly it was believed that badgers only littered every other year. This would be an important reason for seasonal differences in behaviour. Observations in south-west England suggest that this is not the case and that a sow will normally litter every year. Of twenty-five adult females dissected between the end of June and mid-February twenty-three contained either free or implanted blastocysts and embryos. The other two had corpora lutea but no blastocysts.

TYPICAL BEHAVIOUR OF THE ADULT MALE IN RELATION TO THE REPRODUCTIVE CYCLE

The male cub usually leaves the parental set during the autumn of the first year when eight to nine months old. It often lives during the winter in an outlier of the original set either on its own or more often with other cubs of its own age but of either sex. After living as families up to the autumn the adults of one community kept to the breeding sets (A and D) and the cubs went to other holes (B and C) within the same wood about 50 to 100 yards away from the parents. They had moved by December or January:

	A	B	C	D
December 1953	adults	cubs	empty	adults
December 1954	adults	cubs	cubs	adults
December 1955	adults	empty	cubs	adults

The sexes of the adults were not known, but cubs were born at A and D each year, and B and C were only used spasmodically during the summer. If a community becomes large, yearlings appear to move away from the district to find regions of less density.

On approaching maturity wandering becomes more intense and by February is quite marked. Many instances have been recorded during February and March of mature males being killed on roads and railways. Some of these were in out-of-the-way places far from typical badger country. At this season adult males are sometimes flushed from cover above ground by hounds. These are probably animals in a strange district where no convenient sets have been found in which to spend the day.

Probably young males, just mature, mate with young females in smaller and more outlying sets. This impression is gained from watching many such sets and takes into account the small size of the animals. Younger males appear to keep much more to the same district and may be seen over long periods at the same set with the sow. There are many instances of this static behaviour on the part of the male during the period February–May. There is a great deal of movement of mature males during this same period and the new ones to arrive at a community during this time are often very large males. At Cushuish a very large practically white boar (thought at one time to be an albino and easily identified) turned up regularly at one particular hole of set D in February on three consecutive years, but was not seen at any other time of the year. In 1956 at another set there were probably four adults present up to February 5th. On February 7th at least ten were seen (including two female cubs of the previous year). The number remained high until the beginning of May, fluctuating between five and eight adults and including a fairly constant number of sows—two known later to have cubs—and two yearlings. At the same set in 1955 by the first week in April only a single pair of adults were present, but by April 14th the number of adults had increased to eight.

This sudden influx of males points very strongly to the presence in the set of sows which are approaching oestrus. In May 1954 the population rose from three adults (a boar and two sows) on the 14th to six adults (including three or four boars) by the 20th. This was accompanied by a considerable increase in excitement. This also occurred at Cushuish a few miles away where four adults were in residence up to May 12th (two boars and two sows). On the 14th there was much excitement and probably eight adults were seen, including two very large boars not seen previously.

In the period February–May some of the sets scattered over a wide area of country contain up to three sows according to the size of the set. Sometimes the sow is living on her own with her cubs, sometimes with a boar which has mated with her and is static. Immature males and maturing females may be scattered either with adults or on their own. There is also a roving population of adult boars going from one set to another looking for sows coming on heat. This is a very strenuous and full-time activity for the boar. All reserve fat is used up during these months and although there is often plenty of available food, far

less is eaten by the boars than the sows at this time of year. Analysis of stomach contents (Denmark : Andersen, 1955, and Sweden : Notini, 1948) give good evidence that this is so. Their feeding appears to be much more casual and only the more readily accessible forms of food are taken. In Britain food is largely confined to earthworms which may be obtained in quantity relatively quickly on wet nights when they are lying on the surface.

Evidence that feeding is not a main preoccupation during March and April was illustrated on April 18th 1956 when a sow badger left the set at 9.55 p.m., but of the boars present at least three left after midnight. The boar remains near the entrance at this season and often indulges in what is probably displacement activity, especially on evenings of great excitement, by suddenly breaking off after a scuffle to dig out a little loose earth from the set or tentatively collect a small bundle of bedding. Short bouts of digging by the boar during March cannot be compared with the serious excavations made at other times of the year. Sometimes the boar is digging while the sow is bringing in bundle after bundle of dry bracken.

At the time the cubs are born the resident boar, if present, may be banished by the sow from the breeding chamber. The boar usually remains in the same set but uses a different entrance and therefore probably occupies a different part of the underground system. This was suggested by behaviour at Rendcomb and on the Quantocks when from January 28th to February 12th the sow always emerged from one particular entrance while the boars and yearlings nearly always used others. The sow continued to use the same hole (cubs emerged from here later), but in March the other badgers were not so strictly confined to using other holes.

The boar may remain at the set when the sow leaves her young cubs in order to feed. He then goes off when she returns. When cubs are old enough to come above ground the boar plays less part in the social life of the community. Sometimes he is the first to emerge, but more often he is in no hurry to leave. He may play for short periods with the cubs, but more often goes off on his own and does not return until morning. His main activity from mid-May onwards is feeding ; he quickly regains his normal weight and by autumn has stored much extra fat. There are periods in summer and autumn when excitement may become marked and short-duration pairing or attempted pairings have been observed. These periods are marked by much deep purring.

Behaviour of the adult female with cubs

(a) From time of birth until cubs are above ground.

It is difficult to calculate exactly the date of birth of cubs, and hence the behaviour of the sow at the time. Observations at various sets during the first fortnight in February suggest that the sow remains underground then for several nights in succession. When the cubs are very small she leaves the set furtively, usually after other badgers have left. She is extremely sensitive to external stimuli at this period (Neal, 1948), and is not away from the set for long. Often

she is back after an hour, and tends to feed within a short distance from the set. On leaving she sometimes sets scent near the entrance. She appears to take special notice of other badgers and territorial behaviour is now evident (see below).

Much time is spent on bringing back bedding to the set, almost every dry night as many as twenty bundles may be laboriously collected on a single night. This is connected not only with replacement of bedding soiled by cubs, but also as insulation for conserving heat in the breeding chamber. Bedding, sometimes damp, may also be brought in when snow is on the ground. The process of decay of damp hay or bracken may provide useful additional heat. It is significant that much more bedding is brought in during this period than is discarded. Periods of sexual excitement occur during this period, and copulation can take place.

(b) *From the time when the cubs are above ground until weaning starts.*

The sow at this stage is usually in a hurry to leave the set, particularly when the family is large. She is the first to appear at the entrance, and usually goes off before it is dark. She usually returns after 1–1½ hours either to suckle or attend the cubs. This pattern may be repeated at intervals through the night. During a series of complete night watches at Camberley the sow's movements were noted as accurately as possible, the missing data being due to her using another entrance out of view. Typical nights were as follows :

	Emergence	Return
1–2 April 1953	19.45	21.15 G.M.T.
	21.16	21.55
	?	23.15
	2.20	?
21–22 April 1953	20.56	21.52 B.S.T.
	22.10	22.36
	00.03	?
	3.08	4.15
	4.22	4.40
27–28 April 1953	21.00	22.01
	22.02	23.45
	00.51	?
	3.23	4.20

While away from the set the sow was mainly concerned with feeding. During the early part of April a boar was heard purring considerably not far away ; there were many scufflings and vocal noises which suggested sexual excitement. The sow held her tail as if she was on heat. Oestrus may thus occur approximately nine weeks after birth of the cubs. When back with her cubs a considerable amount of low purring by the sow takes place. This appears to be a way of encouraging the cubs to emerge. (See p. 75.)

(c) *Weaning period.*

This lasts about two weeks. The sow leaves her cubs for much longer periods. The cubs are already active and becoming more independent, and regurgitated food is given them (Notini, 1948) to supplement their diet. Otherwise no food is brought back by either parent.

(d) *The summer and autumn period.*

This is the period of feeding up when the sow is independent of her cubs and spends most of the night feeding. She seldom returns to the set during the night.

When weaning is finished it is very usual for the sow with her cubs to leave the set and use another in the neighbourhood. This was noted on several years at Rendcomb (Neal, 1948), and has since been regularly seen at Cushuish, and at another Quantock set. Similar occurrences in other parts of the country suggest that this is a regular feature and serves two purposes. The main breeding chamber is left uninhabited for two or three months, after which it is extensively cleared out and all old bedding removed. This avoids disease and parasites. In large sets it may merely be the leaving of one part of the labyrinth and the using of different entrances, although a complete change of set is more usual.

Another result is a change in food supply. The breeding set is usually chosen in relation to a ready supply of food for the sow during the period when the cubs are small, so that she does not have to leave them for long. This is usually near pasture where earthworms are plentiful. In the summer the diet changes, but the cubs do not wander far as yet, hence a change is made nearer the new source of food. In Pembrokeshire some sets on the coastal cliffs were uninhabited during the winter, breeding taking place inland in more sheltered pastoral areas, but by late May they had moved back to the cliffs where young rabbits and beetles were a major source of food.

Several badger families may live together for a month or more during August and September. This seems to be a characteristic of a population inhabiting an area on which there are several rather small sets close together as at Rendcomb (Neal, 1948), or one very large set as at Cushuish and other Quantock sets. Fourteen badgers (adults and cubs) have been seen emerging from one entrance. They may emerge in succession and follow each other at intervals along a single path to their feeding grounds.

Occasional evenings of excited play occur, but they are not usual. Short-duration pairing may take place on these occasions which may coincide with the ovulations known to occur during the period of delayed implantation. The period is one of intense feeding activity, where the sows behave more individualistically and take little notice of other badgers. Occasionally fresh bedding is brought in and new excavations made, but this occurs more in the autumn.

In the autumn the adult sows tend to disperse to their breeding sets, often to the one they occupied the previous winter. It involves much digging when the set is scoured out and old bedding removed. New bedding is brought back on all suitable nights until a large amount is collected in the chambers.

During November emergence becomes later and less regular, and activity is diminished (see p. 117).

(e) *Winter behaviour.*

Implantation occurs during December or early January, and at this time behaviour is most sluggish. The sow emerges on all suitable nights but may not be out for long. Feeding is spasmodic and during spells of hard frost she may not emerge to feed. On mild nights there may be more activity, and sometimes boar and sow may hunt together over several miles (evidence ; tracks in the snow).

Population density and territory

There is much variation in population density, the highest estimate being three adults per square mile (Neal, 1948) in the Cotswolds. Many other areas of similar density undoubtedly exist. Whether the population is high or low the social structure appears to be of the same type. It consists of a number of scattered communities spaced out according to suitability of habitat and available food, but seldom nearer than half a mile from each other, and usually considerably more than this. Each community consists of a single set (a series of tunnels and entrances which are inter-connected), or several sets rather near together which are occupied at various times of the year by the same badgers.

In typical badger country where density is high, each community may contain up to three breeding sows (Quantocks, 1957). The other members differ somewhat according to time of year. Thus cubs will usually be present during the spring to autumn period, and they may not move until they are yearlings.

The number of boars is also variable. Up to fourteen individuals have been counted at the same community during the summer period. The number of entrances is no indication of the size of the community, as this varies according to ease of digging and man's attempt at blocking up, especially in hunting districts. Twelve badgers were seen to emerge from a set with only one entrance (Eycot, Glos.), and large sets on the Blackdown hills, Somerset, with more than fifty entrances were found to contain fewer badgers.

The home range of each community may overlap that of the next where the density is high. No antagonism or territorial behaviour has been noted in this connection unless the screaming of the badger is interpreted in this way.

Little evidence has been gathered of a true territory, and it appears probable that territorial behaviour is limited to the breeding chamber and possibly its surrounding tunnels and entrances, when the cubs are tiny. Circumstantial evidence from observed behaviour of the sow in relation to other badgers at the breeding season supports this. A fight was witnessed between a sow with cubs underground and another badger which attempted to enter the same set at Camberley.

A sow was seen to set scent at the entrance before leaving a set where she had cubs, which may be a means of marking out her limited territory at that time of year. The leaving of yearling badgers from the parental set may indicate territorial behaviour by the sow as the time of birth approaches.

Choice of breeding set

Over one hundred sets have been investigated, and the following factors appear to be important in the choice of a set.

1. Cover in the vicinity.

Nearly all sets had cover of some kind near some of the entrances. This consisted most commonly of trees and bushes, with thick undergrowth in summer. Elders and nettles were the most characteristic plants near a set. Entrances were occasionally found in open fields, but these were not used regularly and probably acted mainly as bolt holes. Thus woods, copses and hedgerows were the commonest habitats. On cliff slopes where trees were absent, bracken gave most cover. At high altitudes there was a greater degree of exposure and rock fissures were utilized.

2. Slope.

The majority of sets were dug into a slope. Where the country was rather flat, hedgerow banks were often chosen. In other parts quarries, canal or river banks and even railway embankments were used.

3. Soil.

More sets were in sandy soil than in clay although the latter was utilized commonly in districts with little choice. The tunnels usually followed the softer strata, and harder rock was sometimes used as a roof. The sets were always well drained and waterlogged soil and areas subject to flooding were avoided.

4. Altitude.

Most sets were found between 100 and 600 feet above sea level, but instances of over 1,500 feet for breeding sets occur on Dartmoor, in Yorkshire, the Lake District and Scotland.

5. Food supply.

A ready supply of food especially at the breeding season appears to be of great importance in the choice of a set. Most breeding sets were in close proximity to pasture land where earthworms are readily available in the early months of the year when the sow cannot leave the cubs for long (eighteen out of twenty stomach analyses between January and March contained earthworms).

6. Proximity to man.

Badgers avoid using sets for breeding where they are liable to disturbance by man, but where unmolested there are many sets within 100 yards of habitation. In parts where building has rapidly encroached on badger country the animals are still holding their own as isolated communities. This is most evident in the environs of London.

LACTATION AND WEANING

It is probable that the period of lactation is twelve weeks, plus or minus a week. This estimate is arrived at from the following evidence :

1. *Change in behaviour of the cubs.*

Cubs come above ground for the first time when about eight weeks old (range seven to nine). They never move far from the set, and the mother returns at fairly regular intervals during the night (see p. 85). Evidently they are being suckled at this time as they have no opportunity of feeding for themselves ; no food visible to the watcher is brought back by the parents. During the next two weeks the cubs become more venturesome, and soon they are foraging spasmodically. They leave the set for long periods during the next fortnight and spend much time searching for food and by fourteen weeks are independent of the mother. Weaning starts when the cubs are twelve weeks old and it lasts about a fortnight.

Persistent foraging is a sign that weaning has started, and is usually first seen during the first half of May. Most births occur during the first half of February, giving an estimate of twelve weeks for the lactation period.



Fig. 3. Diagram of events in the reproductive cycle of female badgers in south-west England.

2. *Feeding experiments.*

It was found that food put down in the form of bread soaked in dilute honey (K. R. C. N.) was first taken into the mouth and swallowed by cubs about four to five weeks after they were first seen above ground (estimated age eight weeks). A family of cubs, first seen on March 28th 1957, was feeding by May 1st; a second family first seen on April 4th was feeding by May 6th.

It is stated by Notini (1948) that during the weaning period the mother regurgitates food for the cubs.

CHANGES IN THE REPRODUCTIVE ORGANS

(a) *The ovary*

Analysis of events during the ovarian cycle in the badger is considerably facilitated by dividing the specimens available into several main groups, some with subdivisions. Each group comprises animals killed during certain periods of the year; the animals of a group all exhibit certain reproductive characteristics. The main groups are:

- (A) Female cubs.
- (B) Adolescent female badgers killed in early spring.
- (C) Adult female badgers killed in spring and summer.
- (D) Adult female badgers killed in late summer, autumn and early winter.
- (E) Pregnant badgers (excluding those exhibiting delayed implantation).
- (F) Post-parturitional adults with cubs or adults with resorbed embryos.

Separate sections deal with the changes in appearance of the uterine mucosa and vaginal epithelium (pages 106 and 109). Descriptions of the blastocysts will be found on page 111. Reference to the Tables will give brief details about each animal.

A. *The ovary of the cub*

The ovaries of six cubs (see Table 1) aged three to twelve months were similar histologically. Until nearly a year old (B.1-6) the ovary showed little change; it increased slightly in size from about $10 \times 8 \times 8$ mm. to $13 \times 9 \times 9$ mm., and in weight from 0.15 g. to 0.20 g. (Pl. 1, fig. 1).

A thin cortical strip, 100μ thick, was full of oocytes surrounded by a single layer of granulosa cells: there were also a few anovular follicles. The remainder of the ovary was composed of groups of cords of polyhedral interstitial cells separated by connective tissue septa. The interstitial cells averaged 15μ in diameter and the majority contained many small vacuoles. The interstitial cells were larger in some areas and contained one or more vacuoles up to 10μ in diameter. A few healthy and atretic follicles, $50-150\mu$ in diameter, were present. The theca interna was narrow but the interstitial cells surrounding these follicles were enlarged to 15μ in diameter and their cytoplasm was palely stained and contained fine granules. The ovaries of the eleven month old animals contained one to five follicles up to 0.5 mm. in diameter with well-developed antra. The

TABLE 1

Badger Number	Date and place killed	Age and weight	Remarks
B.1	13.6.57 Kingston St. Mary, Somerset	11 weeks 6 lbs	Some precociously enlarged oocytes and multiple follicles
B.2	14.6.47 Wiveliscombe, Somerset	4 months 7 lbs	Female cub of sow B.39. A male cub weighed 9 lbs
B.3	22.6.50 Otterford, Devon	6 months 14 lbs	Two follicles 100 μ
B.4	25.8.53 Clayhidon, Devon	7 months 15 lbs	Two follicles 500 μ
B.5	21.1.50 Bishop's Lydeard, Somerset	11 months 20 lbs	Few small follicles
B.6	23.2.48 Taunton, Somerset	12 months 14 lbs	Thymus 4.0 g.

granulosa layer was four to five cell layers thick and the theca interna, three to four cell layers thick, was clearly discernible. At intervals along the cortex narrow clefts and tubules up to 30 μ in diameter penetrated the cortex and the subcortical region. These tubules were lined by small cuboidal cells which appeared to be in continuity with the covering epithelium of the ovary and with the islands of granulosa cells in the cortical zone. They penetrated some distance into the interstitial tissue and in sections were seen as isolated tubes, cut in cross section, or as narrow clefts some 30–50 μ in length.

Each ovary measured 13 \times 10 \times 10 mm. and weighed about 0.20 to 0.31 g. by the time the female cubs were nearly one year old. There was a clearly differentiated cortical region, nearly 1 mm. thick, which contained lightly staining interstitial tissue aggregated in small cords or columns some 30 to 60 μ in diameter, each surrounded by a thin connective tissue envelope. The medullary interstitial cells contained numerous large vacuoles, some of which were 15 μ in diameter and occupied the entire cell. Vacuolated interstitial tissue was not uniformly arranged, but was present in a series of patches through the ovary. Those cells that lacked vacuoles are more eosinophil and granular than the interstitial cells of the cortex. The tubules of epithelial cells dipping in from the cortex formed a network throughout the cortex and medulla. The cells lining them were low columnar and in places amorphous, granular material was present in the lumen. The intra-ovarian tubules occasionally branched or communicated (Pl. 1, fig. 3).

A few (one to six) follicles up to 0.5 mm. in diameter were present; most were atretic and no theca interna was discernible.

B. Adolescent female badgers killed in early spring

Seven animals (B.7–B.13) were killed between January 23rd and February 25th and are believed from their size, dentition, state of reproductive organs and time of death, to be adolescent females (Table 2). The first four had ovaries each varying in weight from 0.20 to 0.31 g.; B.12 had ovaries weighing 0.44 and 0.43 g. and is believed to be a slightly older female. Badgers 14, 15 and 16 were killed later in the year, but they were either born later than usual (B.14) or were late in becoming sexually mature (B.15 and 16).

TABLE 2

Badger Number	Date and place killed	Age and weight	Remarks
B.7	23.1.53 Otterford, Devon	About 1 year 20 lbs	Several follicles up to 1.0 mm.
B.8	31.1.57 Grange-over Sands, Lancashire	About 1 year 19 $\frac{3}{4}$ lbs	Several follicles up to 1.0 mm.
B.9	6.2.57 Devizes, Wilts.	1 year 23 lbs	Few follicles up to 100 μ
B.10	7.2.57 Alton, Hants.	1 year 21 $\frac{1}{2}$ lbs	Three follicles 1.0 mm.
B.11	11.2.44	Not known	Two follicles 2.0 mm. In early oestrus
B.12	24.2.57 Bath, Gloucester	27 lbs	Probably in second year
B.13	25.2.54 Taunton, Somerset	1 year 16 lbs	Seven follicles 1.0 mm.
B.14	5.5.48 Norton Fitzpayne, Somerset	15 months 14 lbs	Either late in becoming mature or born late. Thymus 6.5 g. Four follicles 0.5 mm.
B.15	16.6.57 Kingston St. Mary, Somerset	About 15 months 24 lbs	See text. Few follicles 100 μ
B.16	19.12.54 Blagdon, Somerset	In second year 24 lbs	See text

The majority of the ovaries in this group contained from one to four large healthy follicles varying in diameter from 1.0 to 2.0 mm.; B.12 had only small primordial follicles. Numerous atretic and lutealized follicles were present.

Follicles from 100 μ to 600 μ were frequent (six to ten in each ovary); many were atretic. All possessed a well-differentiated theca interna some four to six cell layers thick. Its cells were large, 15–20 μ in diameter, and often with granular, vacuolated cytoplasm. There were also a number of lutealized follicles 0.5 mm.

in diameter devoid of antra. The ovaries were well-vascularized and the vessels engorged with blood. The three animals killed later in the year (B.14, 15, 16) showed less ovarian activity. B.16 was probably older than the others and nearing the end of its second year.

The appearances of ovary, uterus and vagina (pp. 106, 109) suggest that female badgers reach puberty shortly after they are one year old. Changes of pro-oestrus can be seen in the reproductive organs at the age of eleven to twelve months, but may be delayed until fifteen months or later.

C. Adult female badgers killed in spring and summer

This group includes adult females of this series killed between mid-February and mid-June. It can be subdivided into four smaller groups depending on whether the animals possessed corpora, were lactating or contained ova in their uterine tubes or blastocysts in their uterine horns. Evidence of recent pregnancy was assessed by examination of the uterus, presence of cubs in the same set and active mammary tissue. The uterine horns were all carefully examined for blastocysts and, where available, the uterine tubes were serially sectioned and searched for ova. Ova and blastocysts may have degenerated after death. One horn of the uterus of a badger known to contain blastocysts in the other was, however, left unopened for two days and blastocysts were easily located but were collapsed. The four subdivisions of this group are as follows :

- C.1. Adult female badgers that had ovulated but from which *no* ova or blastocysts were recovered and which were *not* lactating.
- C.2. Adult badgers that had ovulated, which possessed ova in their uterine tubes or blastocysts in their uterine horns but which were *not* lactating.
- C.3. Adult badgers that had ovulated, which were lactating, but from which no ova or blastocysts were recovered.
- C.4. Adult badgers that had ovulated and were lactating and from which blastocysts were recovered.

Group C.1.

All twelve animals in this group were killed between March 1st and June 15th and had corpora (range 2-12 per pair of ovaries ; average number per animal = 4.33). No eggs or blastocysts could be found in the uterine horns or in those uterine tubes that were serially sectioned. The uteri showed no indication of recent pregnancy ; mammary glands were inactive and nipples small.

In each animal all corpora appeared to be of the same generation, except in B.18 and 23. The former was killed on March 10th ; the ovaries contained five recently ruptured follicles 3 mm. in diameter with fluid filled central cavities up to 2 mm. across. The mural lutealizing granulosa layer averaged 0.8 mm. in thickness. The granulosa cells were elongated, little endothelial invasion had occurred and theca interna cells were arranged about the periphery of the gland. There were also seven old corpora 1.0 to 1.5 mm. in diameter. They were of two types ; one contained palely stained, vacuolated luteal cells and had been

invaded by connective tissue ; the second contained fewer, more densely stained luteal cells and many leucocytes. The ovaries of B.23, killed on May 4th, contained seven corpora. Two appeared younger (for criteria see later) and might have belonged to a second generation.

TABLE 3

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.17	1.3.44	Adult	3 ; old	Four follicles (3-4 mm.) about to ovulate
B.18	10.3.54 Cambridge	Not known	12 ; 7 old, 5 young	Recently ovulated : ovaries only available
B.19*	14.4.52 Ilminster, Somerset	Large adult	3 ; involuting	
B.20*	30.4.55B Clayhidon, Devon	Young adult 15½ lbs	2 ; established	
B.21*	29.4.56 Luppit, Devon	Young adult 19 lbs	3 ; established	
B.22	1.5.49 Wiveliscombe, Devon	Young adult 18 lbs	5 ; established	
B.23*	4.5.53 Clayhidon, Devon	Young adult 18 lbs	7 ; established	(Two corpora appeared to be younger)
B.24*	12.5.53 Clayhidon, Devon	Adult 25 lbs	4 ; young	Living with an adult male
B.25	15.5.56 Burford, Oxford	Young adult 18 lbs	3 ; involuting	
B.26	27.5.53 Clayhidon, Devon	Young adult 21 lbs	3 ; young	Recently stopped suckling
B.27*	9.6.53 Clayhidon, Devon	Adult 23 lbs	4 ; young	
B.28	15.6.54 Clayhidon, Devon	Adult 23 lbs	3 ; established	Two 2.0 mm. follicles

* Uterine tubes serially sectioned and searched for eggs.

Details of the corpora in the other badgers are given in Table 3. They varied in that some (B.26 and 27) appeared to be about a week old, others (B.20, 21, 22, 23, 24 and 28) were more established but not markedly active, and yet others (B.17, 18, 19 and 25) showed varying degrees of involution. The youngest corpora were 3.0 mm. in diameter, had thin capsules or theca externa and large

cores of palely stained, cellular connective tissue. Luteal cells were elongated, arranged radially, and were up to 20μ in length and $5-10\mu$ broad. Their cytoplasm was palely stained, granular, with few vacuoles and their nuclei showed varying degrees of vesiculation. A few endothelial sprouts had developed into the gland, but the degree of vascularization was poor. Small theca interna cells were randomly distributed at the periphery.

Established corpora were $3.0-3.5$ mm. in diameter, had thicker capsules, and a more organized central core of connective tissue. Luteal cells were polyhedral and $12-15\mu$ in diameter; the cytoplasm was granular, eosinophil, but with few vacuoles. Their nuclei were 4μ in diameter, but showed little vesiculation. Many luteal cells contained sparsely distributed brown or yellow pigment granules. A striking feature was its poor vascularity; few large vessels penetrated the capsule and capillaries were sparse. Large veins or sinusoids were absent. What vessels were present were not engorged with blood.

Involutionary changes in the corpora involved shrinkage, fragmentation and heavy vacuolation of the luteal cytoplasm; nuclei had become pyknotic. There was invasion by connective tissue elements, small round cells and leucocytes. These changes had only advanced far in the old corpora of B.17 and 18; in the others such retrogressive changes were limited only to certain areas. Each gland was poorly vascularized and histochemical methods did not indicate marked secretory activity. The corpora of B.17 and 18 showed the greatest degree of involution; they were between 1.2 and 1.8 mm. in diameter. Luteal cells had degenerated, many contained vacuoles or had fragmented. There was marked invasion by connective tissue which had become well organized. Both ovaries of B.17 contained ripe, healthy follicles from 3.5 to 4.0 mm. in diameter (four in all). The oocytes ($115-125\mu$ in diameter) had broken free from the follicle walls. Comparison with other ovaries indicates that the corpora lutea were at least several weeks old, suggesting that ovulation had occurred at the end of January (see p. 115) and that a second ovulation could have occurred shortly after the time of death had the animal remained alive.

The badgers in this group are young or full-grown adults and have all ovulated recently—i.e. within the previous month at least. This would mean that ovulation can occur from the end of January until June. The failure to recover ova or blastocysts from these animals suggests that the corpora lutea were either the result of infertile matings or that ovulation can occur spontaneously. The corpora are too poorly developed to be those of a previous pregnancy except perhaps in B.17 and 18 (see above); in any event there was no indication that these badgers had been pregnant recently (except B.25, which had recently stopped suckling). The absence of ova in the genital tracts is not surprising if it is assumed that they had not been fertilized; the corpora were all of an age beyond which it is not believed that unfertilized ova can survive.

Group C.2.

This group includes those badgers killed in the spring and summer (February 16th to June 5th) that possessed corpora (range $3-7$ per pair of ovaries; average per

animal=3.83) and in which ova or blastocysts were recovered. The animals had not been recently pregnant; none was lactating but B.34 appeared to have ceased suckling fairly recently.

TABLE 4

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.29	16.2.52 Bishop's Lydeard, Somerset	Adult 26 lbs	7 ; 4 old	Two ova in right tube
B.30	9.3.57 Alton, Hants.	Adult 25 lbs	3	One blastocyst 1.0 mm. diameter
B.31	1.4.57	Young adult 15 lbs	3	One blastocyst (lost)
B.32	30.4.55 A Clayhidon, Devon	Young adult 16 lbs	3	Three blastocysts, one transmigrated
B.33	1.6.54 Clayhidon, Devon	Young adult 15 lbs	3	Three blastocysts. Two follicles 3.0 mm. <i>In oestrus</i>
B.34	5.6.54 Clayhidon, Devon	Adult 20 lbs	4	One blastocyst ; recently stopped suckling

B.29 shows that ovulation can occur in the middle of February (see p. 78). No blastocysts were found in the horns, but two one-celled eggs were found in the right tube. They appeared degenerate as the ooplasm was heavily vacuolated; the zona pellucida was intact but few corona radiata cells were adherent. They were probably unfertilized oocytes (see Notini, 1948). The left ovary contained a recently ruptured follicle 2.5 mm. in diameter (Pl. 2, fig. 3) and a healthy follicle 3.0 mm. in diameter with its oocyte (130μ zonal diameter) free in the antrum. The right ovary possessed two recently ruptured follicles; stigmata were still discernible. In the recently ruptured follicles a large fluid-filled central cavity was surrounded by a layer of granulosa cells 150μ thick. Early changes of lutealization had occurred and endothelial invasion of the membrana granulosa had begun. Luteal cells were fusiform, $12-15\mu$ in length; no vacuoles were present in the cytoplasm and no nuclear vesiculation had occurred. Both ovaries had two much-shrunken corpora albicantia in each; these were under 1.0 mm. in diameter. They were encapsulated structures composed of a few heavily vacuolated luteal cells but mainly of fibrous tissue and some small round cells. In view of the difficulty of assessing the rate of involution of corpora (see p. 105) it is probable that these corpora albicantia result from a previous pregnancy. The uterine mucosa was thin and showed little evidence of secretory activity; the appearances of the vagina are described on p. 109.

B.30 and B.31 each contained a single small blastocyst (1.0 mm. in diameter) in the uterine horn. These are the earliest records (March 9th and April 1st) of recovery of blastocysts. Each animal had a total of three corpora which were 3.0 mm. in diameter and possessed a central core of young connective tissue; all showed similar histological features. Vascularization was marked; the capillaries and young sinusoids were engorged with red cells. Small vessels ran radially through the gland dividing it into segments; some branching of these vessels occurred within the gland, giving it the appearance of large islands of luteal cells within capillary networks. Luteal cells were elongated, granular and devoid of cytoplasmic vacuoles.

B.32 and B.34 possessed three corpora and three blastocysts and four corpora and one blastocyst respectively. One of the blastocysts in B.32 appeared to have transmigrated to the left side. The corpora had a similar appearance and, apart from being less well vascularized, were like those described above. The mammary glands of B.34 had recently ceased activity; there were no signs of any retrogressing corpora albicantia. The three corpora in excess of the number of blastocysts in this animal could represent persistent corpora of pregnancy; their appearances do not suggest it, however, and see p. 105.

B.33 possessed three corpora and three blastocysts; one of the latter had transmigrated to the left side. The right ovary contained two mature follicles 3.0 mm. in diameter. The corpora were well established and 3.0 mm. in diameter, but poorly vascularized. Luteal cells were slightly to heavily vacuolated; the vacuoles were mainly small, about 1μ in diameter. Numbers of shrunken, densely eosinophil luteal cells with pyknotic nuclei were distributed throughout the gland. They were reminiscent of similar cells found in corpora of other mammals (Corner, 1945; Harrison, 1948) at a time that coincides with hormonal adjustments (p. 117).

Group C.3.

This group comprises those badgers that possessed corpora (range 3–5 per pair of ovaries; average per animal=4.0) and were known to be *lactating*. No eggs or blastocysts were recovered from any of them.

TABLE 5

Badger Number	Place and date killed	Age and weight	Corpora lutea	Remarks
B.35	11.3.54 Ilminster, Somerset	Young adult 20 lbs	4	Lactating
B.36	25.3.57 Taunton, Somerset	Adult 29 lbs	4	Lactating
B.37	10.5.54 Clayhidon, Devon	Young adult 18 lbs	3	Lactating
B.38	11.5.56 Luppit, Devon	Young adult 23 lbs	4	Lactating
B.39	14.6.47 Wiveliscombe, Somerset	Young adult 15 lbs	5	With two cubs probably being weaned

The appearances of the uterus of B.35 suggested that it had littered two to three weeks before death. Four similar corpora were present (2.0–2.5 mm. in diameter). Some luteal cells were large, 20μ in diameter, and heavily vacuolated; others were fragmented or had lost their nuclei. Connective tissue invasion had occurred and many leucocytes were present.

B.36 had two dark congested patches in each uterine horn that suggested it had recently given birth. The animal was lactating. The right ovary contained four fairly recent corpora 3.0 to 3.5 mm. in diameter. All had a large central core of connective tissue. There were also at least two structures in the ovaries resembling those believed to be corpora albicantia described on p. 96. The younger corpora had luteal cells 15μ in diameter, with granular cytoplasm, many were fusiform. Vascularization was poor.

B.37 and B.38 were lactating animals that had respectively three and four young, but established corpora in their ovaries. All possessed young central cores of connective tissue, luteal cells had granular cytoplasm and lacked vacuoles. There were no corpora albicantia.

B.39 was killed with two cubs, but it is not known if it were lactating. The ovaries contained five corpora of similar appearance and with central cores of connective tissue. Luteal cells were 15μ in diameter and had granular cytoplasm. A few had fine cytoplasmic vacuoles (Pl. 2, fig. 4).

It is assumed that the corpora of B.35 are those of the previous pregnancy showing involutionary changes. If the small atretic structures described in the ovaries of B.36 are corpora albicantia, and represent the corpora of the previous pregnancy then it follows that there had been post-parturient ovulation.

Group C.4.

Two badgers were *lactating* when killed at the end of May and in early June, and contained corpora and blastocysts.

TABLE 6

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.40	22.5.54	Young adult 16 lbs	6	Lactating 2 blastocysts
B.41	8.6.51	Adult 29 lbs	4	Lactating 3 blastocysts

B.40 possessed six corpora, all of similar appearance, and two blastocysts. The corpora were 3.0 mm. in diameter, well developed, but poorly vascularized and with sparse connective tissue. Luteal cells were $12\text{--}15\mu$ in diameter and their cytoplasm was finely vacuolated. There were no corpora albicantia. The central core of connective tissue was better organized and more densely stained in two of the corpora, but these were the only features that could suggest that these corpora were the older.

B.41 possessed at least four corpora of similar appearance and at least one retrogressing corpus albicans (the ovaries were incomplete). Three blastocysts were present in the left uterine horn. The four corpora were similar in size and histology to those of B.40. The corpus albicans was 0.5 mm. in diameter and was surrounded by remnants of the theca externa capsule. A few shrunken, pyknotic luteal cells and some leucocytes were scattered amidst fibrous tissue strands. Many brownish pigmented droplets were distributed throughout the structure. Several luteal cells contained numerous fine droplets of a similar pigmented material. It is assumed that this represents one at least of the retrogressing corpora of pregnancy.

D. Adults killed in late summer, autumn and early winter

All the badgers in this group possessed corpora and, except three, had blastocysts in the uterine horns. Only one, B.45 killed on August 4th, 1954, showed evidence of lactation. The group may be sub-divided on the basis of whether the number of corpora equalled the number of blastocysts or whether it was greater ; it was never less. The group is sub-divided thus :

- D.1. Animals in which the number of corpora equalled the number of blastocysts.
- D.2. Animals in which the number of corpora was greater than the number of blastocysts.
- D.3. Animals that possessed corpora but from which no blastocysts were recovered.

Group D.1.

This small group includes those badgers killed in September and October in which blastocysts were recovered and in which there was an equal number of corpora (range 2-5 per pair of ovaries ; average per animal=3.66).

TABLE 7

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.42	14.9.55 Clayhidon, Devon	Adult 25½ lbs	4	4 blastocysts-ovulated recently. One blastocyst had transmigrated
B.43	30.9.53 Clayhidon, Devon	Adult 26 lbs	5	5 blastocysts, one degenerate
B.44	4.10.47 Langport, Somerset	Adult 26 lbs	2	2 blastocysts

B.42 had four corpora (3.0 mm. in diameter) each with a small fluid-filled central cavity (Pl. 3, fig. 6) ; only one was in the right ovary. The right uterine horn contained two blastocysts, presumably one had transmigrated. The polyhedral luteal cells were closely packed, averaged 15μ in diameter, and their cytoplasm contained a few minute vacuoles. The gland was poorly vascularized ; no

connective tissue invasion had occurred. The glands are about eight to ten days old and provide evidence that fertile mating can take place in early September.

The corpora of B.43 and B.44 were better established than those described above. They were all 3.0 mm. in diameter and possessed well organized central cores of connective tissue. Luteal cells averaged 15μ in diameter and contained many small vacuoles. All corpora were better vascularized than in B.42, but no connective tissue had invaded them. Both ovaries of B.43 contained many small follicles and two of 2 mm. None of the ovaries of these two animals was completely sectioned serially; it is not impossible that there were additional corpora.

Group D.2.

This large group comprises fifteen badgers killed between August 4th and December 12th in which the number of corpora (range 4–11 per pair of ovaries : average per animal=6.8) considerably exceeded the number of blastocysts (range 1 to 4 : average per animal=3.0).

The majority of the 103 corpora present in these fifteen pairs of ovaries were remarkably similar in appearance. They varied in size from 1.0 to 2.5 mm., but most were 2.0 mm. in diameter. They possessed distinct capsules of fibrous tissue varying in thickness from 20 to 75μ . Large blood vessels penetrated the capsule or ran within it for short distances. All corpora possessed distinct central cores of connective tissue up to 1.0 mm. across (Pl. 3, fig. 5). Luteal cells were closely packed at the periphery, but were often loosely arranged near the central core. They were usually polyhedral, were 12 or 15μ in diameter, and had numerous fine vacuoles distributed evenly throughout their cytoplasm. No large vacuoles like those found in the corpus of pregnancy (p. 104) were observed. The cytoplasm was eosinophil and finely granular. The vesicular nuclei were 4 to 6μ in diameter. No traces of theca interna cells could be discerned. All corpora were poorly vascularized; capillaries extended radially towards the centre from the vessels in the capsule, dividing the luteal cells into groups of some ten to twenty cells. Many anastomotic loops and connections had been formed around these cell groups. Every corpus was alike in that there was little or no blood within its vessels. Little connective tissue had invaded the glands, and no leucocytes were observed within the fabric.

Attempts were made to discern differences in age of these corpora based on various criteria. Overall size of the gland, thickness of the theca externa, size and density of the central core of connective tissue, degree of vascularity and characteristics of luteal cells were all compared, but none provided a reliable feature that could be correlated with age. It was impossible to assess the relative ages of the majority of corpora.

One curious feature was the apparent nuclear degeneration that was present in the whole or in part of certain corpora (B.52, B.53 and 54). Both luteal and endothelial elements were devoid of stained nuclei and the luteal cytoplasm was heavily vacuolated. It is considered that these must be corpora that had suffered post-mortem changes; it is presumed that they were less stable, and perhaps older than their neighbours and succumbed more easily to autolytic changes

TABLE 8

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.45	4.8.54 Burnham, Somerset	20 lbs	4	Two blastocysts ? lactating ? had very late cubs
B.46	25.8.53 A Clayhidon, Devon	23 lbs	5	Two blastocysts
B.47	25.8.53 B Clayhidon, Devon	Adult 24 lbs	4+	Three blastocysts
B.48	7.9.54 Clayhidon, Devon	Adult 27 lbs	9	Three blastocysts
B.49	15.9.53 Clayhidon, Devon	27 lbs	5	One blastocyst
B.50	16.9.54 Clayhidon, Devon	25 lbs	5	Two blastocysts; follicles 2.0 mm., in oestrus
B.51	3.10.54 Clayhidon, Devon	Adult 29 lbs	11	Four blastocysts. One follicle 3.0 mm.
B.52	16.10.54 Kingston, Somerset	Adult 32½ lbs	9	Three blastocysts. Ova in tubes : recently ovulated
B.53	20.10.54 Washford, Somerset	Young adult 21 lbs	9	Four blastocysts
B.54	24.10.54 Clayhidon, Devon	Young adult 21 lbs	6	Four blastocysts
B.55	26.10.55 A Thornfalcon, Somerset	Young adult 26 lbs	4	Two blastocysts
B.56	26.10.55 B Thornfalcon, Somerset	Adult 25 lbs	8	Four blastocysts
B.57	1.11.52 Wiveliscombe, Somerset	Adult 32 lbs	8	Four blastocysts
B.58	5.11.55 Bath, Somerset	Adult	10	Four blastocysts
B.59	12.12.54 Clayhidon, Devon	Adult 31½ lbs	6	Three blastocysts

after death. Support for this view is provided by the absence of any markedly degenerating corpora in any of the animals killed later in the year or after implantation had occurred. In several of the well-fixed corpora of delay, numbers of degenerating cells were present in the central region. Their cytoplasm was densely stained, shrunken or "fibrous" in appearance, and their nuclei were pyknotic or fragmenting. It would appear that the gland was not sufficiently established to support its total luteal cell population. It was as if these corpora

were in a state of suspended activity and were only just being maintained as histological entities. Further evidence of death of luteal cells during delay is provided by examination of the corpora of early pregnancy (p. 104).

Several ovaries contained healthy developing follicles (1.0 to 3.0 mm. in diameter). B.46, 47, 50 and 51 all had follicles nearing maturity and in the latter two the vaginal epithelium was thick and stratified.

B.52, killed on 16.10.54, is of particular interest. Three healthy blastocysts were present in the uterine horns. The ovaries contained a total of nine corpora lutea of which five appeared similar to those described early in this section. Another four had ruptured only a short time before death. They measured 2.5 mm. in diameter and possessed large fluid-filled central cavities (Pl. 4, fig. 1). The mural lutealizing granulosa layer was 0.5 mm. thick and its cells were mainly elongated. Early endothelial invasion was occurring at its periphery. These corpora were essentially similar to those described in B.29, killed on 12.2.52, and appeared so young that the only available uterine tube, the right, was sectioned. Two degenerating ova (Pl. 4, fig. 2) were found; the zona pellucida was intact, but distorted, and corona radiata cells were still arranged about it. The ooplasm was heavily vacuolated and no nucleus was present. For these reasons it was thought to be unfertilized. Ovulation can thus occur at a time that would seem to be late in the period of delay.

Group D.3.

This group includes five animals killed between September and January which contained corpora but in which no blastocysts were found. They were not lactating.

TABLE 9

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.60	29.9.54 Clayhidon, Devon	Adult 26 lbs	9	
B.61	29.9.46 Stoke St. Mary, Somerset	Adult	3 at least	Incomplete specimen, there may have been blastocysts
B.62	5.10.57	Adult 28 lbs	4	
B.63	25.10.55 Ashfordby, Leicester	Young adult	3	
B.64	7.1.52 B Netherstoway, Somerset	Adult 31 lbs	8	

B.60 contained nine established corpora, all of which had a central core of connective tissue. The smaller central cores of two corpora looked older judged by the darkly stained, densely packed collagen fibres. The luteal cells of all corpora were closely packed, except at the centre, where they were separated by

intercellular fluid. The luteal cells were 15μ in diameter and contained fine cytoplasmic vacuoles. The degree of vascularization was much as in the specimens described in Group D.2. There was no connective tissue invasion. Both ovaries contained many dilated cysts lined by a simple epithelium.

B.61 was an incomplete specimen ; at least three corpora were present in one ovary. It is not known for certain whether or not there were blastocysts in the uterus. The corpora were similar to those described above, as were the four in B.62 and the three in B.63. The uterine horns of B.63 had been fixed before examination ; the uterine tubes were serially sectioned but no eggs or blastocysts were found. Both B.61 and B.63 could have contained blastocysts, but lack of evidence necessitates placing them in this group. Both contained in their ovaries numbers of healthy and atretic follicles up to 1.0 mm. in diameter. It would seem that all three animals had ovulated some weeks before death ; one at least, B.60, appeared to have two sets of corpora of different ages.

B.64, killed on 7.1.52, was the only animal obtained in January that was not pregnant. Eight corpora were present in the ovaries ; they showed signs of retrogression and numerous leucocytes had invaded the gland.

Group E.

This group includes all those badgers with embryos and fetuses, but excludes all those exhibiting delayed implantation. Six pregnant (one to four fetuses) adults were killed in January. Several ovaries were received incomplete, so the total number of corpora is not known. The number per animal was, however, usually greater than that of blastocysts.

TABLE 10

Badger Number	Date and place killed	Age and weight	Corpora lutea	No. of fetuses	Length in mm.
B.65	7.1.52 A Netherstoway, Somerset	Young adult 29 lbs	7	4	40
B.66	10.1.55 Halse, Somerset	Adult 28 lbs	9	3	20
B.67	20.1.52 A Netherstoway, Somerset	Adult 28 lbs	11	4	82
B.68	20.1.52 B	Young adult 20 lbs	2	1	80
B.69.	23.1.49 Bishop's Lydeard, Somerset	Young adult 25 lbs	7	4	30
B.70	25.1.53 Branscombe, Devon	Adult	?	3	120

The youngest fetuses (20 mm.) were found in B.66. The ovaries contained nine corpora of which eight measured 4.0 mm. and one 1.0 mm. in diameter. Luteal cells measured $25-30\mu$ in diameter and possessed finely vacuolated perinuclear cytoplasm. Peripheral cytoplasm was densely eosinophil and granular. The gland was poorly vascularized with little invasion by connective tissue. Large numbers of granular and agranular leucocytes were present: in the centre of the gland each luteal cell was surrounded by an almost continuous layer of them. The central core of connective tissue was no longer present; only a few, if any, strands of collagen remained (Pl. 5, fig. 4).

B.69 was pregnant with four fetuses 30 mm. in length. There were said to have been seven corpora on external examination but incomplete material enabled only four (3.5-4.0 mm. in diameter) to be examined histologically. Luteal cells were large, 30μ in diameter, with vesicular nuclei 9μ in diameter. They were all heavily vacuolated: some contained one large vacuole. The gland was poorly vascularized, little connective tissue was present and only few leucocytes. The central core of connective tissue was absent.

B.65 contained four fetuses 40 mm. in length, externally there appeared to be seven corpora in the ovaries. Histological preparations were only available of two glands, both from the left ovary. Their characteristics were exactly like those of B.69, but they were better vascularized. A capillary network extends throughout the gland enclosing groups of three to six luteal cells in its loops.

B.67 and B.68 were killed on the same day, and contained four 82 mm. fetuses and one 80 mm. fetus respectively. There were seven corpora in the left and four in the right ovary of B.67. Histological examination of two corpora showed little significant difference from B.65. B.68 possessed one corpus luteum in each ovary; each was similar in appearance to those described above except that there were more leucocytes.

B.70 was pregnant with three 120 mm. fetuses and was estimated to be near term (p. 73). It was not known how many corpora were present; one only (3.0 mm. in diameter) was available for histological examination. Luteal cells averaged 25μ in diameter were palely stained and were heavily vacuolated. Some cells contained many small vacuoles, others two or more large vacuoles almost occupying the entire cell. Many central luteal cells had fragmented and degenerated; numerous leucocytes had invaded the gland in the centre. The degree of vascularization was comparable to that of previous specimens, little connective tissue invasion had occurred. No central core of connective tissue was present (Pl. 5, fig. 5).

Group F.

The badgers in this group are known to be either immediately post-parturient, or to have been pregnant but in which the embryos had died and were being resorbed.*

* A young adult sow was received from Horsham, Sussex on 6.2.58, after this paper had been completed. It weighed $24\frac{1}{2}$ lbs and was not lactating. It had recently aborted; at least three placental sites were obvious. There were eight corpora which showed retrogressive changes similar to, but not as advanced as, those seen in B.72.

TABLE 11

Badger Number	Date and place killed	Age and weight	Corpora lutea	Remarks
B.71	5.2.57 Alton, Hants.	Young adult 20½ lbs	4	Three resorbed conceptuses
B.72	6.2.55 Clayhidon, Devon	Young adult 20 lbs	6	With three cubs
B.73	27.3.56 Yorkshire	Adult	3+4 old	Caught with its three cubs

B.71 had two swellings (1.5 cm. in diameter) in the right uterine horn and one (0.75 cm.) in the left horn. They contained remnants of resorbed embryos: only a few trophoblast cells remained viable. Four corpora were present on the left (4.0, 3.0, 3.0, 2.5 mm. in diameter). All showed advanced signs of involution. Luteal cells were palely stained, many were heavily vacuolated or fragmented, some had a "fibrous" appearance. Many leucocytes had invaded the gland and fibroblasts were widely distributed. There was no central core of connective tissue. All glands were well vascularized, the vessels had thicker connective tissue sheaths than those in most other corpora and were engorged with blood.

B.72 had three large post-parturient swellings (2.5 cm. in diameter) in the right uterine horn and was apparently caught immediately after birth of its cubs. Lactation had not obviously commenced. The right ovary contained six retrogressing corpora, all less than 2.0 mm. in diameter. Luteal cells were very palely stained with heavily vacuolated cytoplasm and pyknotic nuclei. Many luteal cells had lost their nuclei and were mere "ghosts". Much round cell and polymorphonuclear leucocytic invasion had occurred, connective tissue invasion was also marked. These corpora all appear to be involuting rapidly. Numbers of follicles (6 of 1.0 and 1 of 3.0 mm. diameter) were present.

B.73 was caught with three cubs estimated to be a minimum of three weeks old and was suckling them (Nettleton, 1957). Three corpora were present, 3.5 mm. in diameter, and luteal cells were both elongated and polyhedral; the latter were mostly 15 μ in diameter. They were eosinophil, granular and had only fine vacuoles in the cytoplasm. A marked core of young connective tissue was present. The gland was poorly vascularized and some connective tissue had invaded them. Also present were at least four structures considered to be corpora in advanced stages of involution. They were 0.5 to 1.0 mm. in diameter and had marked fibrous capsules. Numbers of obliterated blood vessels extended through the capsule. The structures contained many fibroblasts, and numbers of luteal-like cells full of brownish pigmented vacuoles. A few leucocytes were also present. It is suggested that these structures represent the much-involuted corpora of pregnancy and that the other three corpora are the result of recent ovulation. This suggests that corpora of pregnancy involute within about three weeks and that a post-parturient ovulation can occur at least within fourteen days of parturition. It is, however, possible that the cubs were somewhat older than three weeks.

Ovariectomy during delay

The adult female B.74 was captured alive on 13.5.56 and kept in a pen with a younger female for several weeks. It was later separated and kept in isolation in another pen. Bilateral ovariectomy was performed on 3.9.56. under continuous sodium thiopentone anaesthesia. The right ovary contained three corpora lutea, the left two. The uterine horns were uniformly slender and did not exhibit localized swellings, oedema or hyperaemia.

TABLE 12

Badger Number	Dates captured and killed	Age and weight	Remarks
B.74	Caught Taunton, Somerset, 13.5.56 Killed in captivity 14.11.56	Old adult 32 lbs at death	Ovariectomy 3. 9. 56. 5 corpora. 5 blastocysts recovered at death

The five corpora were 2.8 to 3 mm. in diameter and were all histologically similar. A central core of young connective tissue was present in each. Luteal cells were polyhedral, some 20μ in diameter, and had granular eosinophil cytoplasm. The glands were poorly vascularized (Pl. 5, fig. 1).

The animal was killed on 14.11.56, ten weeks after ovariectomy and twenty-five weeks after capture. The uterus was opened immediately and five large blastocysts (p. 113) were observed at the distal ends of the uterine horns (Pl. 4, fig. 5). The uterine mucosa was about 0.5 mm. thick and appeared well vascularized; the cellular stroma was not oedematous. The glands were 30μ in diameter, few possessed a lumen. The gland cells were low columnar and had scanty palely stained cytoplasm. Some pale eosinophil material was present in most ducts. The lining epithelium was low columnar 15μ high; the cells had densely stained, compact nuclei (Pl. 5, fig. 2).

The vaginal epithelium was transitional and 30μ thick. In many areas the superficial layer was low columnar and nuclei were pyknotic (Pl. 5, fig. 3). Leucocytes were sparsely distributed throughout the sub-epithelial zone, but were densely aggregated into clumps in some regions.

These observations indicate that blastocysts must have been present in the uterus for at least twenty-five weeks and that ovariectomy near the middle of this period does not materially affect them (p. 113).

(b) *The uterus and uterine mucosa**In cubs and adolescent badgers*

The uterine horns increased in diameter from 1.5 mm. at eleven weeks of age (B.1) to 4.5 mm. at one year (B.6). The mucosa was thin ($150\text{--}200\mu$), devoid of glands and covered by low cuboidal epithelium for the first five months. The mucosa was then $300\text{--}400\mu$ thick, an indefinite stratum compactum was present, short primitive glands were appearing and the epithelium was pseudo-stratified (B.3). The developing straight glands had extended through the mucosa by

eleven months (B.5). They were 0.5 mm. long, 40μ in diameter and possessed a lumen by the time the cub was a year old.

The uterine horns of badgers over a year old (Group B) varied in diameter from 3.0 to 5.0 mm.; the mucosa was from 0.5 to 1.0 mm. thick. Glands showed varying degrees of development, but were always straight and generally possessed a lumen (Pl. 2, fig. 1). They were from $40\text{--}50\mu$ in cross-sectional diameter, their nuclei were situated in the basal part of the gland cells. The glands appeared inactive. The lining epithelium was between 10 and 20μ high, usually low columnar. In many specimens narrow, densely stained basophil cells were interspersed among the broader columnar cells. There was some variation in the degree of development of the mucosa in this group. The uteri of B.7, 10 and 15 were larger than the others, better vascularized, with their vessels dilated with blood and had a taller lining epithelium.

In animals in oestrus and after ovulation

B.17 had four large follicles in its ovaries: the uterine mucosa was 1.0 to 1.25 mm. thick. The glands were straight, $40\text{--}60\mu$ in diameter, with nuclei centrally placed in the gland cells; some glands contained secretory product. The stroma was oedematous and some leucocytes lay below the uterine epithelium. The latter was 15μ high, mainly columnar but with occasional basophil fusiform cells included within it.

The general appearances of the uterine mucosa of B.29 (two ova recovered from the uterine tube) and of all the animals in Group C.1 were similar to those just described for B.17. The lining epithelium showed the greatest variation. In most specimens it was as described above, but in B.21, 24 and 27 it was high columnar and presented a "palisade" type of epithelium. The cells were up to 40μ in height, with vesicular nuclei basally situated and with palely stained cytoplasm. None of the specimens were markedly oedematous or hyperaemic.

The uterine mucosae of the animals in Group C.3 and D.3 were essentially similar: there was variation in the height of lining epithelium. B.63 exhibited the most marked palisade type of cell, B.62 presented the lowest lining epithelium.

During the period of delayed implantation

This section includes most of the animals in Group C.2 and all those in Groups C.4, D.1 and D.2. All the mucosae were similar: their folds varied between 1.0 and 1.5 mm. in thickness. The glands were straight, 40μ in diameter, and most lacked a lumen. Secretory droplets were present in the mouths of others. The gland cells had centrally placed nuclei; but there was no evidence of active secretion. The stroma was cellular and uniformly dense and was not oedematous; little fibrous tissue was present. Blood vessels were not conspicuous and were not engorged with blood.

The only clearly discernable changes were those in the lining epithelium. This was consistently of the tall columnar, palisade type, its cells varied in height from 25 to 45μ . The cytoplasm was palely stained. The vesicular nuclei varied

from basal to superficial in position within each cell, not only from area to area but also in each specimen (Pl. 2, fig. 5, and Pl. 3, fig. 3).

The uterine mucosa of B.42 exhibited the most pronounced secretory activity. The animal had corpora lutea, with small fluid-filled central cavities, estimated to be eight to ten days old. Secretory products filled the ducts and terminal parts of the glands: the basal portions lacked a lumen and appeared inactive. The mucosa was moderately oedematous and more hyperaemic than any other obtained during delay. The lining epithelium was relatively low (20μ), however, and stained densely.

The consistent appearance of the mucosa during the period of delay in implantation is one of the striking features of the reproductive changes in the badger. Even in B.59 (killed near the time implantation should occur) the uterine mucosa presented an appearance little different from that early in the period of delay.

During and after pregnancy

Dramatic changes occurred in the mucosa after implantation and during establishment of the placenta (B.66 and 69). The mucosa was at first thickened and markedly hyperaemic. The glands mouths were dilated to 300μ . The mucosa thinned as the placenta developed, but the remaining basal portions of the coiled glands were enlarged (100μ across) and flattened. They were secreting actively.

B.71 was killed on 5.2.57; very degenerated remnants of three conceptuses were found in the uterus, histologically few embryonic tissues could be recognized. The inactive mucosa was 0.3 mm. thick and many leucocytes were present in embryonic remnants and mucosa. The incomplete epithelial lining was low columnar.

B.72 and 73 were both post-parturient animals. The uterine horns exhibited swellings at the placental sites. Repair of the mucosa had progressed slightly in B.72, and was complete in B.73. It was 3 mm. thick in B.72 and the stroma had a fibrotic, hyaline appearance; some stromal cells were vacuolated, others were degenerating. The lining epithelium was low columnar where present, remnants of necrotic placental tissue were still attached to the placental site. The glands were $45-60\mu$ in diameter, many contained debris consisting of granular basophil material and leucocytes. All glands showed involutionary changes, many of their cells were degenerate, others were small and palely stained. Many leucocytes were distributed throughout the mucosa; they were most abundant in the sub-epithelial zone. Obliterated, thick-walled blood vessels were present in many areas. The mucosa of B.73 was much like that described for the post-ovulatory group (p. 107). The stroma was fibrous, but not hyaline or oedematous. The glands were inactive; the lining epithelium was low columnar. Histiocytes containing small pigmented granules were distributed throughout the mucosa and there were remnants of obliterated blood vessels. The appearances suggested that several weeks had elapsed since parturition.

(c) *The vagina*

The vaginal epithelium was two to four cell layers thick in cubs and adolescent animals. The sub-epithelial tissue was cellular and contained few leucocytes. By the age of one year (B.9) the epithelium was four to five layers thick and was transitional. Some leucocytes were present within the epithelium and were aggregated into clumps in the immediate sub-epithelial region. The majority of the animals in Group B had similar epithelia (Pl. 2, fig. 2); B.10, however, had a stratified squamous epithelium 150μ thick. The superficial layers were not cornified; but appearances were those of early oestrus.

B.17 had a thick ($250\text{--}500\mu$) stratified squamous epithelium. Little cornification had occurred, flattened nuclei were present in the most superficial cells. Few leucocytes lay in the sub-epithelial zone. The animal appeared to be nearing full oestrus. B.29 was in full oestrus and its epithelium was slightly thicker than B.17, but superficial layers were cornified and were sloughing. Of the remainder of the post-ovulatory non-pregnant Group C.1 all except B.17 showed marked epithelial sloughing and the sloughed cells occupied the lumen of the vagina in clumps. Some leucocytes were present in the sub-epithelial zone of most specimens; in B.26 and 27 (Pl. 2, fig. 6) there had been a profuse invasion and dense aggregations were arranged at close intervals. B.19 had a low four-layered transitional epithelium, few sub-epithelial leucocytes were present, and sloughing had occurred some time earlier.

B.36, of Group C.3 (animals that have ovulated during lactation but are not pregnant) was actively sloughing its epithelium. Few sub-epithelial leucocytes were present; the blood vessels were large and were engorged with blood. B.35 and B.37 had a low transitional epithelium, some remnants of much degenerated epithelial cells were present in the lumen with a few leucocytes. B.38 had remnants of degenerated, desquamated cells in its lumen, but the epithelium was stratified squamous and was 100μ thick. No cornification had occurred.

B.30 and 31, from Group C.2 (with blastocysts in the early part of delay) had partially or completely sloughed epithelia (Pl. 3, fig. 2). The latter exhibited only a low ragged epithelium, repaired in places as transitional. Few leucocytes were present. B.33 exhibited a dramatic difference (Pl. 3, fig. 1); the epithelium was thick (300μ) and stratified. No cornification of the superficial cells had occurred. This specimen had mature follicles and corpora and healthy blastocysts.

The vaginal epithelia in Groups D.1 and D.2 (during the period of delay) varied considerably in appearance. B.42, 43, 45, 46, 55 and 59 possessed a three to five layered epithelium 25 to 50μ thick. It was typically transitional in appearance, with leucocytes only rarely present and few in the sub-epithelial zone. No desquamated cells or leucocytes were present in the vaginal lumen.

B. 49 had an epithelium much like those above, but the superficial layer was composed of tall columnar cells up to 25μ in height. This change has been described by Harrison *et al.* (1952) in Pinnipedia.

The epithelium was strikingly different in B.50, B.51 and B.52. The greater part was 200μ thick and was stratified squamous in B.50. The superficial layers showed slight cornification, some sloughing of this layer had occurred in isolated

areas. Both B.51 (Pl. 3, fig. 4) and B.52 had a similarly thick epithelium, but considerable sloughing had occurred from the ventral vaginal wall. Numbers of leucocytes were present in the sub-epithelial zone.

In B.48 and 56 the vagina was filled with dense clumps of desquamated epithelial cells. The residual epithelium was only two to three cells thick and presented a ragged edge. Many leucocytes were present in the sub-epithelial zone and among the desquamated cells. B.57 and 58 had much degenerated remnants of a few epithelial cells together with some leucocytes in the vaginal lumen. The epithelium was two to three layers thick and was being repaired into a transitional type.

Group D.3 contains five animals killed between September and January which had corpora, but in which no blastocysts were found. B.60 showed advanced sloughing with pronounced and extensive leucocytic invasion of the sub-epithelial zone. B.62 showed some sloughing, but changes were not marked. B.63 had a low transitional epithelium.

The vaginal epithelium was $80-100\mu$ thick in early pregnancy (B.66 and 69 only available). It was transitional in parts, but in most of its extent the superficial layer was transformed into high columnar, mucified cells some 30μ in height.

B.71, in Group F, had a low, ragged transitional epithelium. No cells were present in the vaginal lumen; few leucocytes were in the sub-epithelial zone. B.72 had a thick ($120-150\mu$) stratified squamous epithelium which was not cornified. This animal had recently given birth, yet its ovaries contained several developing follicles (p. 105). B.73 was about three weeks post-parturient and had ovulated between this time and its death. The vaginal epithelium showed advanced sloughing, a moderate number of cells were present in the vaginal lumen. The residual epithelium was mostly low and ragged, but in areas it was low transitional.

THE TESTIS

Fourteen male badgers, killed in the region of Taunton, Somerset, have been examined; the weights of testes and epididymides and other details are given in Table 13.

Examination of sections of testes and epididymides suggests that by about fifteen months (M.3, Pl. 1, fig. 4) active sperm formation has been initiated.* No evidence of active sperm formation was seen in the tubules ($60-100\mu$ in cross sectional diameter) of a cub aged about five months (M.1) or of one aged eight months (M.2). In the younger cub interstitial tissue was marked (Pl. I, fig. 2) and present in aggregated clumps of cells $12-15\mu$ in diameter with granular cytoplasm. Animals M.5 and M.6 were adults nearing maturity; slight to moderate spermatogenesis was present and a few spermatozoa had collected in the epididymis.

* It is not certain that M.3 was exactly fifteen months old. External examination suggested that it was in its second year: it was living alone with B.22 (p. 94), a young adult, which possessed established corpora lutea.

TABLE 13

DETAILS OF MALE BADGERS

Animal Number	Date killed	Approximate age	Weight of both testes (g)	Weight of both epididymides	Remarks
M.1	5.8.54	Cub	1.22	1.22	
M.2	15.10.55	8 months	4.50	—	Inactive
M.3	1.5.49	15 months 23 lbs	4.40 (one only)	—	Early activity some sperm in epididymis
M.4	27.1.56	Adult	16.64	4.96	*Active
M.5	11.2.57 B	Young adult	11.05	3.36	Slight activity
M.6	11.2.57 A	Young adult	12.03	3.28	Moderate activity
M.7	20.2.54	Young adult	10.40	3.4	*Active
M.8	12.3.55	Young adult	—	—	*Active
M.9	29.3.54	Young adult	20.25	5.85	*Active
M.10	17.7.56	Young adult	11.90	—	*Active
M.11	14.9.55	Young adult	12.70	—	Active
M.12	24.9.55	Young adult	—	—	Slight activity
M.13	17.10.55	Young adult	22.00	—	Slight activity
M.14	12.12.56	Young adult	12.75	3.3	Slight activity

* Indicates massive accumulation of spermatozoa in the epididymis.

Badgers M.4 and M.7–M.14 were adult. The average cross sectional diameters of the seminiferous tubules are given in fig. 4, which also indicates those animals which contained massive collections of spermatozoa in the epididymis. It will be seen from this figure and Table 13 that the testes are active from late January until July at least. There is a decline in activity in late September (M.11 : Pl. 1, fig. 6) and it is not until January that full activity is restored. Weight of the testes alone is little guide to activity : the heaviest organs are from M.9 (very active) and M.13 (little activity) and those of M.7 (very active : Pl. 1, fig. 5) are lighter than those of M.14 (inactive).

DELAYED IMPLANTATION AND THE BLASTOCYST

Fries (1880) was the first to record unimplanted blastocysts in a badger, killed on October 16th 1878 in Germany. Fischer (1931) examined ten animals which contained unimplanted blastocysts, the latest date being January 29th, although he also found early implantation stages on January 2nd. The earliest recovered was on July 30th. A mature female killed on August 6th had none, but mature follicles were present. Hence he assumed that the mating time was July–August and the duration of delay four to five months. Notini (1948) in Sweden showed that free blastocysts were present as early as May 20th. He considered this month as the normal mating time, and January as the usual time for implananation.

In this series from south-west England a 1 mm blastocyst was present as early as March 9th, and others in April. It is probable that ovulation and fertilization occur even earlier. Long-duration mating was observed on February 10th and ova were found on February 16th (B.29).

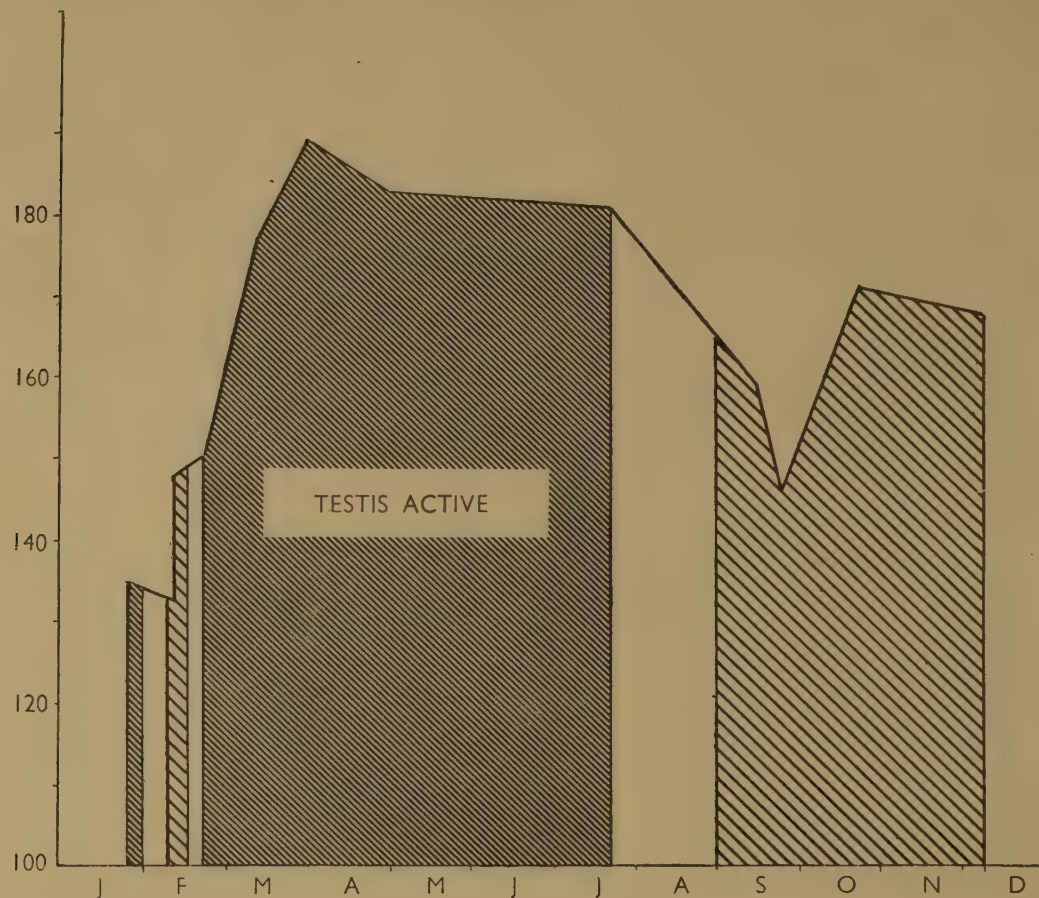


Fig. 4. Table to show the average diameters of seminiferous tubules from testes of animals killed January to December (see Table 13). The dark hatching indicates full testicular activity with marked storage of epididymal spermatozoa; the lighter hatching indicates reduced testicular activity with few spermatozoa in the epididymides.

A total of seventy-three blastocysts was recovered from twenty-five animals (range=1 to 5 per animal, average per animal=2.92. Average number of fetuses in pregnant animals=3.16). The overall zonal diameter of unfixed and fixed blastocysts were estimated as the mean of three measurements (fig. 5): the blastocysts were frequently flattened or collapsed. Many blastocysts showed post-mortem changes, but there was no reason to suppose that they were degenerate at the time of death. The zonal diameter of blastocysts recovered towards the end of the period of delayed implantation is two to three times greater than that of those recovered earlier. The zonal diameters of four of the blastocysts from

B.74 ovariectomized ten weeks before death are greater than that of any recovered from normal animals (Pl. 4, figs. 3, 4 and 5).

There was a large fluid-filled perivitelline space in all blastocysts, whether fixed or unfixed, and probably a post-mortem change. Fixation caused some shrinkage of the blastocyst, and frequently distorted the zona. The latter was thin ($2-4\mu$) and was easily dented. It was thickest in the blastocysts recovered in early delay and thinnest in those of B.74.

The perivitelline space was estimated to be 70–80 per cent of the total zonal volume. The blastocysts were all spherical, but in many the outline was irregular. Trophoblast cells could be clearly seen and varied in diameter from 60 to 100μ . The maximum diameter of the trophoblastic sphere was slightly, but not significantly larger at the end of the period of delay ($0.5-0.57$ mm. in early June to $0.58-0.64$ mm. in December), but it was considerably larger in the five blastocysts of B.74 after ovariectomy ($0.88, 1.16, 1.28, 1.36, 1.40$ mm. respectively).

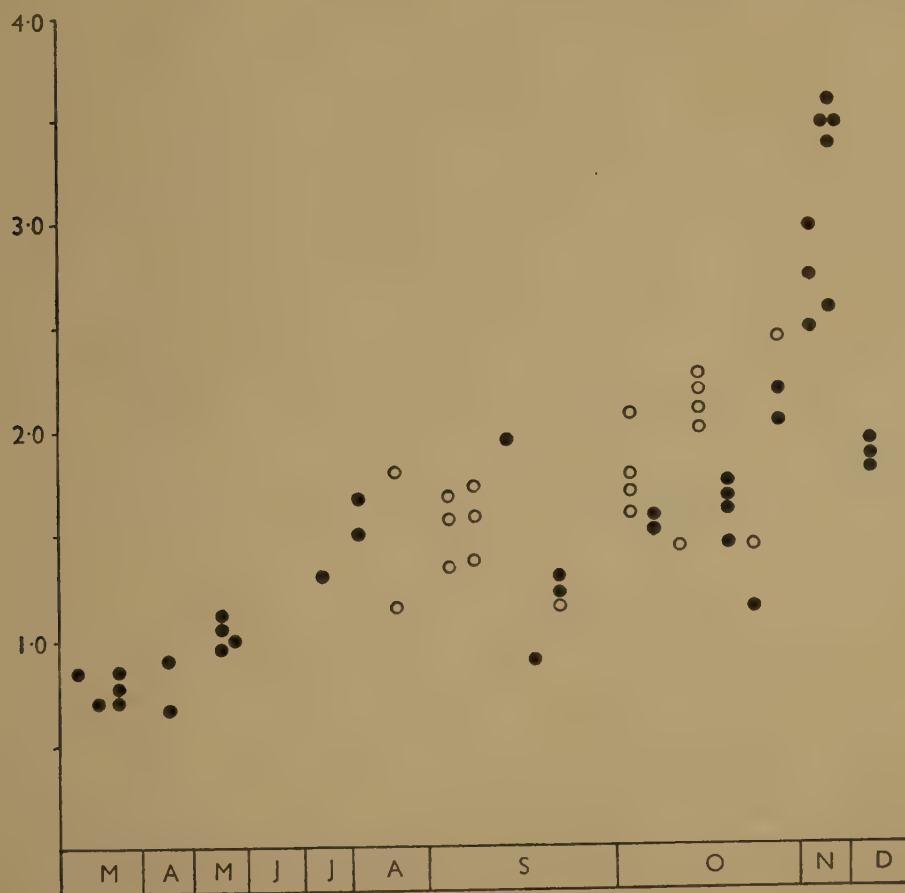


Fig. 5. Average zonal diameters of blastocysts recovered from the uterus during delayed implantation (March to December). The four at the top right, and the one directly below, are those from the ovariectomized animal B.74. The clear circles indicate some collapse of the zona at the time of measurement.

The trophoblast was a single layered hollow sphere in all specimens. The inner cell mass was about 0.1 mm. in diameter and hung inside the blastocyst cavity attached to a slight depression on the trophoblast. It was somewhat everted in a few blastocysts and caused the trophoblast to project.

Estimates were made of the number of cells in the trophoblast. After calculation of the total surface area and measurement of individual cells, the following figures were obtained :

B.33, obtained 1.6.54.

Three blastocysts, diameters, 0.5 and 0.52 mm.

Estimated number of cells in trophoblastic sphere=890, 935 and 985.

B.59 obtained 12.12.54.

Three blastocysts, diameters, 0.58, 0.59 and 0.59 mm.

Estimated number of cells in trophoblastic sphere=2,000, 2,051 and 2,120.

B.74 killed 14.11.54, ten weeks after ovariectomy

Five blastocysts, diameters 0.88, 1.16, 1.28, 1.36 and 1.40.

Estimated number of cells in trophoblastic sphere=2,471, 4,415, 5,325, 5,977 and 6,380.

DISCUSSION

Extensive behavioural observations, together with the representative series of specimens examined, have enabled us to make a fairly confident analysis of the pattern of reproduction in badgers in south-west England. The series is unfortunately deficient for certain important periods, but this does not necessarily affect the conclusions. It does, however, prevent any elucidation of mechanisms that may terminate delay in implantation. The reproductive pattern of *Meles meles* is complicated and is not necessarily similar in any two females. Reference should be made to Hansson (1947) and Enders (1952) for description of somewhat similar events in mink and to Baeyevski (1955) in sable.

Female, and probably male, badgers reach maturity during their second year. What follows depends on factors which are the primary causes of variation in the reproductive pattern. The time of birth in any year affects the time of onset of maturity in the subsequent year. An animal born in February may exhibit a pattern of events in its second year quite different from that in a cub born in the late spring or summer. Events in older females appear to be influenced by the time of year at which parturition occurs. There is some evidence that not all females are pregnant every year.

Our findings suggest that the length of *lactation* does not affect the time of implantation. The majority of badgers in south-west England have ceased lactating by the end of June and implantation does not occur until five months later. Blastocysts were recovered in May and June from two lactating animals and not from three others (but see Canivenc & Laffargue 1956, 1957 a and b). The age of the adult female has no definite influence on the reproductive pattern exhibited, both old and young females show great variation.

All females display a sequence of events that falls between two extremes, bearing in mind the factors mentioned above. Animals may ovulate as early as

February and exhibit follicular activity with vaginal cornification and further ovulations in June, September or October; implantation occurs in November, December or January. By contrast animals may ovulate for the first time in September or October with implantation again in the November to January period. Ovulation early in the year may not necessarily be followed by fertilization; many female badgers killed in the spring had ovulated but did not possess blastocysts. The male can be active and fertile at this time. Accumulation of corpora lutea as the result of successive ovulations explains the large number in animals killed after September which have only few blastocysts.

Up to June the number of corpora in most animals approximates closely to that of blastocysts (average 4.2; twenty-five animals) although in some it is greatly exceeded (B.18). Those with higher numbers are animals in which a further batch of follicles has developed and further ovulations taken place.

During the period July–December the numbers of corpora had risen significantly to 6.2 (twenty-one animals) but the number of blastocysts per animal had not increased appreciatively (2.6 for February–June: 3.0 for July–December).

The corpora lutea of pregnancy retrogress rapidly after parturition and there is a postparturient ovulation within a few weeks. The corpora lutea of delay are remarkably ill-developed (p. 100), poorly vascularized and show little evidence of secretory activity (see Harrison *et al.* 1952). Some even show signs of retrogression or degeneration during the latter part of delay. Corpora of pregnancy are larger, better vascularized and appear active. Several early corpora of pregnancy contained an unusual number of leucocytes. These may result from localized degeneration of corpora during delay. There is no doubt that the corpus after implantation is subject to a strong rejuvenating stimulus. There is no direct proof of progesterin secretion from corpora after implantation, but lack of reaction of uterine glands during delay (p. 107) and their subsequent marked activity throughout pregnancy is significant. Whether the adrenal plays any part cannot be assessed from our material. The histology of the adrenal cortex, adrenal weights and histochemical changes are too variable and unreliable to allow any statement.

Comparison of reproductive changes with those of mating behaviour is possible. Variation in behaviour from very short to very long matings suggests that only long duration pairings result in fertilization (cf. other mustelids). All but one long pairing (out of eight) occurred between February and May; the exception being in September. Short duration pairing occurred from February–May and Mid-July–October. This evidence and the fact that the majority of adult females contain blastocysts by June suggests that spring is the fertile mating period. Notini (1948) has presented evidence that copulation induces ovulation in captive females. Most adults examined between February and June had corpora, but only a few also contained blastocysts. More might have had blastocysts which had degenerated post-mortem. The corpus luteum of pregnancy degenerates rapidly and most of the animals in the above group were not lactating and showed no sign of having been recently pregnant. It is concluded that short duration pairings may be instigating pseudo-pregnancy. Hansson (1947) and Enders (1952) showed

that in mink riding without copulation might elicit pseudo-pregnancy. It is quite possible that in early spring some males are either not fully mature, or that the testis is variable in becoming seasonally active. We, at least, are not yet fully convinced that the female badger does not exhibit a subdued and prolonged, but nevertheless distinct, cycle, and that ovulation may not be spontaneous.

One or more oestrous periods can occur in females when healthy blastocysts are present in the uterus. Ripe follicles are found in animals killed in June, August and September and on October 16th a female was killed with old and very young corpora present, and also unfertilized ova in the tube while healthy blastocysts were in the uterus. The vaginal picture of these animals is typical of oestrus, although little change is seen in the uterine histology.

A large number of short-duration pairings (or ridings) has been seen during the mid-July–September period and these coincide with oestrous periods. This would account for the further ovulations and the increase in the number of corpora characteristic of the second half of the delay period.

If *all* animals had a second oestrus the ratio of corpora to blastocysts in July–December would be expected to be about double that for February–June. This is not the case (6.2 : 4.2). But 1. Some animals have late litters and hence a late first oestrus (B.42). 2. Some young animals are late in becoming mature. 3. Failure of fertilization following first matings would boost the number of corpora during the first half of the delay period.

The majority of adult females in our series had blastocysts by June ; only one adult ovulated for the first time in September (B.42). This could be associated with the occasional observation of long duration pairing in September (Howard, 1956).

Delayed implantation.

Fischer (1931) and Notini (1948) considered that true pregnancy lasted seven to eight weeks. If this assumption is correct, implantation may take place as early as November as early January births have occurred. In south-west England the first half of February is the usual time for birth, making December the normal time for implantation. The variation in the time of implantation from mid-November to end of January is not due to seasonal differences, as animals living in the same locality may give birth to cubs at very different times (a five week difference was noted in 1957, Quantocks).

We are confident that the period of delay must vary in different animals from nearly ten months (early fertilization), to as short as two or three months (autumn fertilization). We have no evidence that time of implantation varies with time of fertilization or is influenced by the age of the animal. To these figures we must add the seven to eight weeks of true gestation time to get the full figure from fertilization to birth i.e. four to nearly twelve months.

The latter figure tallies well with older records of animals captured as adults and subsequently kept in isolation. 'The Field' (1860–67) published record of a female kept isolated for forty-six weeks and five days before giving birth. Another caught on April 3rd 1860 gave birth to two cubs on March 12th 1861 after more than eleven months. F. Heycock told of a badger which produced young thirteen

months after capture, and J. Freeland reported from the Hull zoo that one gave birth to four young after fifteen months isolation. We consider that these abnormally long periods may be due to increase in the delay period due to conditions of captivity. It is well known that badgers captured as adults mope and behave abnormally : captivity may well upset the conditions necessary for implantation.

It is difficult from our material to be dogmatic about factors influencing the onset of implantation. We do not agree with Canivenc & Laffargue (1956, 1957) that lactation affects the time of implantation. Even in those badgers ovulating in September (and lactation has never been observed later than August) implantation is at least two months later. We do agree, however, that implantation does not appear to be due to accumulation of a particular number of corpora. An animal may possess equal or an increased number of corpora at the time of implantation.

Neither Canivenc & Laffargue (1957 b) nor Buchanan *et al.* (1956) were able to procure implantation in badgers or armadillos by injection of hormones (progesterone and oestrogens) during delay. Hansson (1947) was unable to precipitate implantation in mink during delay by administering progesterone with or without small amounts of oestrogen.

Hansson (1947) found that if ovariectomy were performed in mink before administrations of progesterone implantation was promoted. Buchanan *et al.* (1956) found that ovariectomy in the middle period of delay in armadillos resulted in implantation one month later without administration of hormones. In a single badger in this series healthy, enlarged, unattached blastocysts were found ten weeks after ovariectomy. Several workers have remarked on an increase in size of blastocysts just before implantation (Notini 1948, Canivenc & Laffargue 1957 a), but the appearance of the uterine mucosa of the above animal did not suggest impending implantation.

The influence of light on implantation in feral badgers has been discounted by us (Harrison & Neal, 1956), but it is known to be a factor in some other mammals (Pearson & Enders, 1944 ; Hansson, 1947 for references). Notini (1948) has suggested that climate can influence implantation : he claims that implantation in Swedish badgers takes place in January (one month later on average than in south-west England). The American badger (*Taxidea taxus*) usually gives birth in February at sea level in the west of the United States, but in the mountains not until April-May and thus must implant later at higher altitudes (Grinnell, Dixon & Linsdale, 1937). Births in north Britain occur later than in the milder south-west (Neal, 1948).

Activity in the field diminishes during December, when implantation usually occurs. Animals in captivity may also be markedly inactive at this time (personal observations). True hibernation in badgers does not occur in this country, but the animal spends less time above ground during early winter. This period of diminished activity could be looked upon as a period of "least stress". Indeed stress has been shown to be an experimental factor retarding implantation in rats (Canivenc & Mayer, 1955 a and b) and see also Shelesnyak, 1957 for observations on mechanism of ova-implantation in rats). Badgers in captivity, captured as adults, could be considered to be living under conditions of mild stress : it is

in such captive animals that record periods of delay have been noted.

Reference has been made to a rise of temperature (14° F) in, or more probably near, the nesting chamber during winter: this could be associated with the simultaneous diminished activity due to colder seasonal conditions. Delay may be prolonged abnormally in animals kept in captivity without a nesting chamber. Reduced activity associated with a rise in temperature in the environment of the nesting chamber are at least two important factors precipitating implantations.

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SUMMARY

1. An analysis is given of observations on the life history and reproductive biology of the badger in southern England.

2. Characteristics of the cub, time of birth, its behaviour and age at reaching sexual maturity are described.

3. Mating behaviour and variations in the pattern are given. Long duration mating usually occurs most frequently February–May: short duration mating occurs then and again during July to October.

4. Observations on lactation suggest that it usually lasts three months and has ceased in most animals by the end of May.

5. Change in the ovary, uterus and vagina have been examined in over seventy adult badgers.

6. Ovulation may occur as early as February; blastocysts were recovered from uterine horns from March until December. The number of corpora lutea is significantly greater than the number of blastocysts in many animals.

7. Delayed implantation lasts from two to ten months: ovulation may occur more than once during delay.

8. The uterine mucosa maintains a characteristic appearance throughout delay: the vaginal epithelium passes through a striking cycle(s) during delay correlated with ovarian events.

9. Implantation usually occurs in December; parturition in February (seven to eight weeks true gestation period); average number of cubs is 3.0.

10. Examination of the testes from fourteen males suggests that male cubs reach puberty in the second year. The testes are active from January until at least July, less active from October to December.

11. The discussion is concerned with the variations in the reproductive patterns and the factors that may influence implantation.

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PLATE 1

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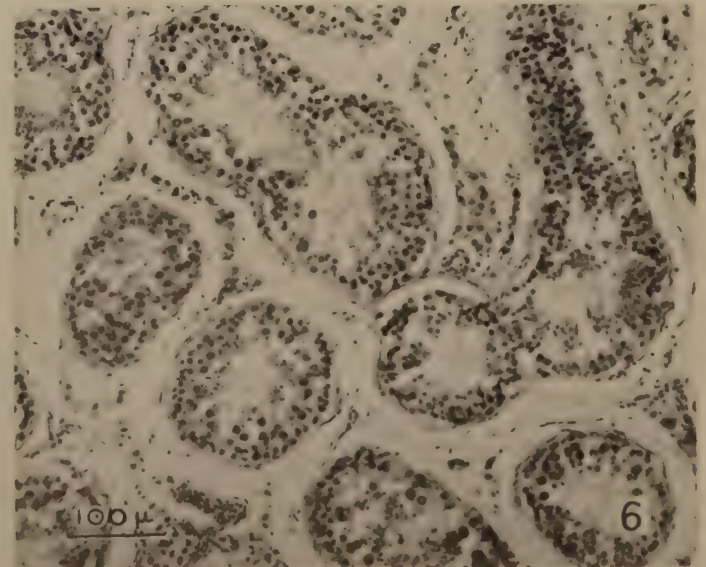
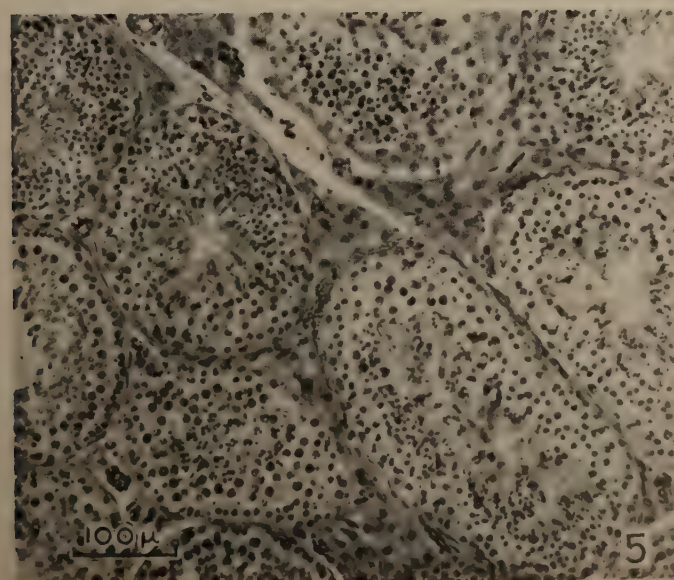
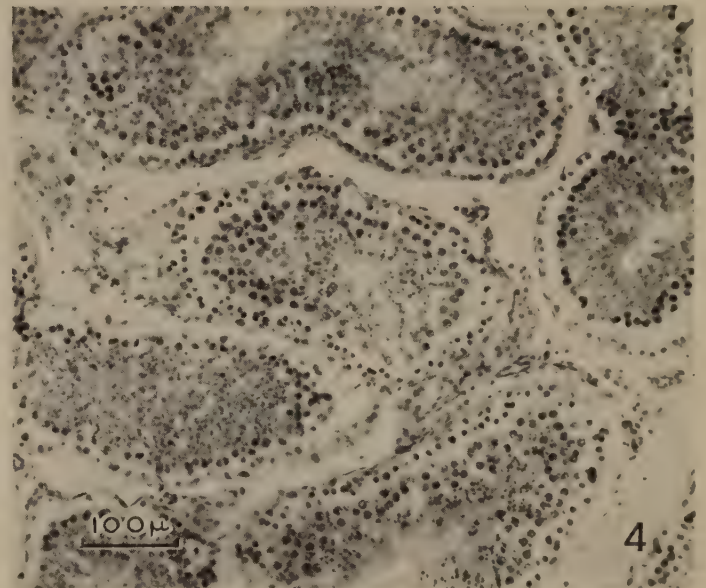
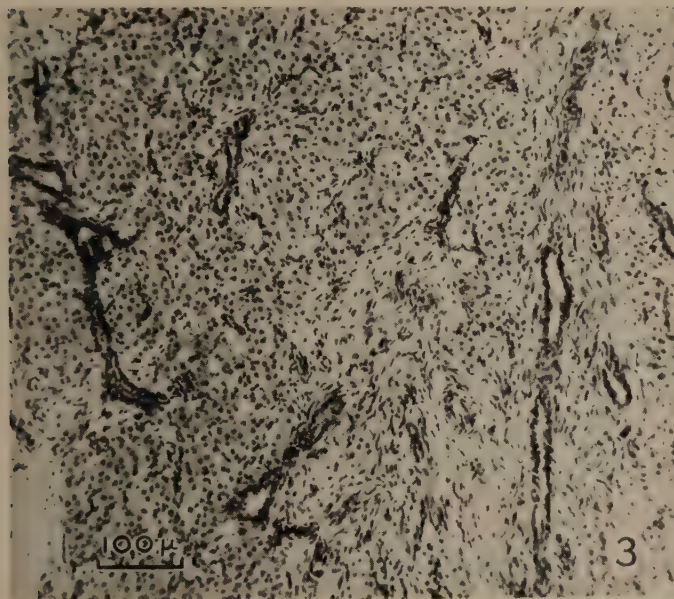
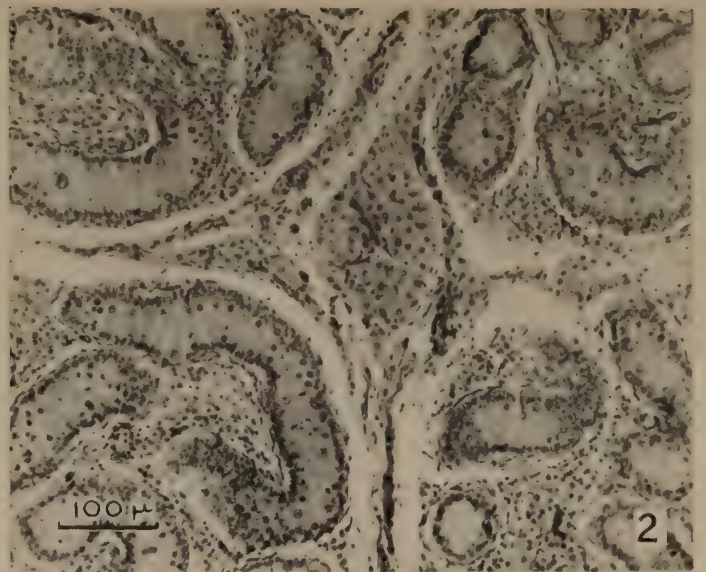
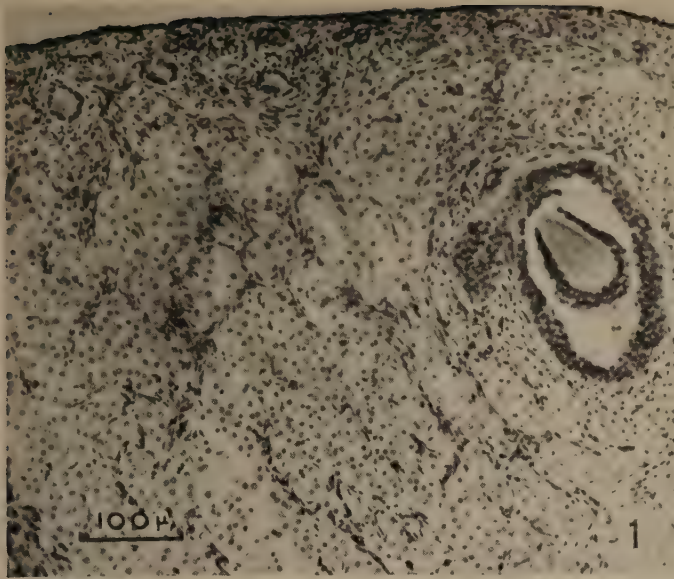


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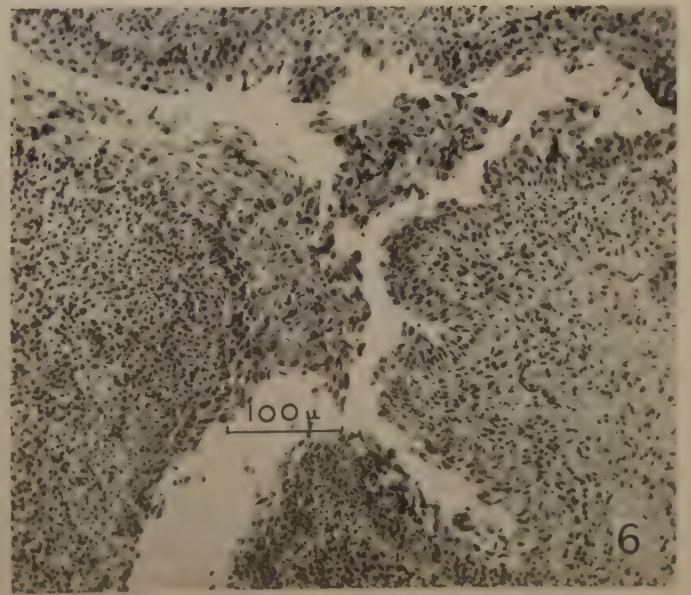
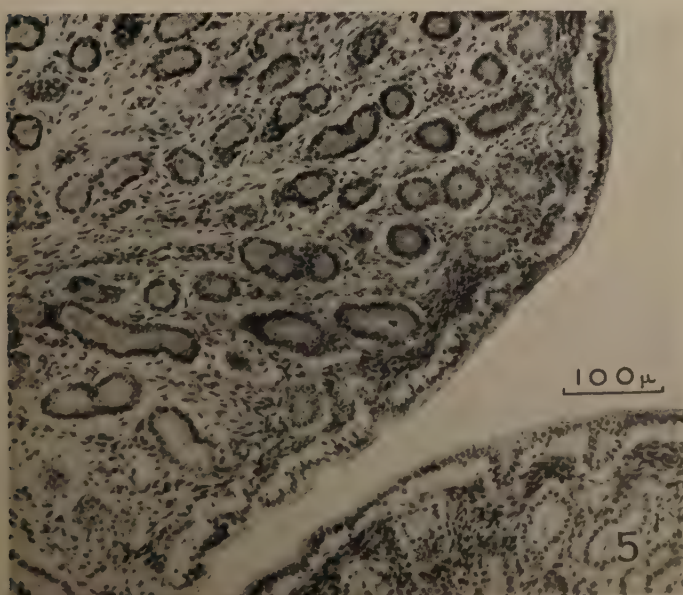
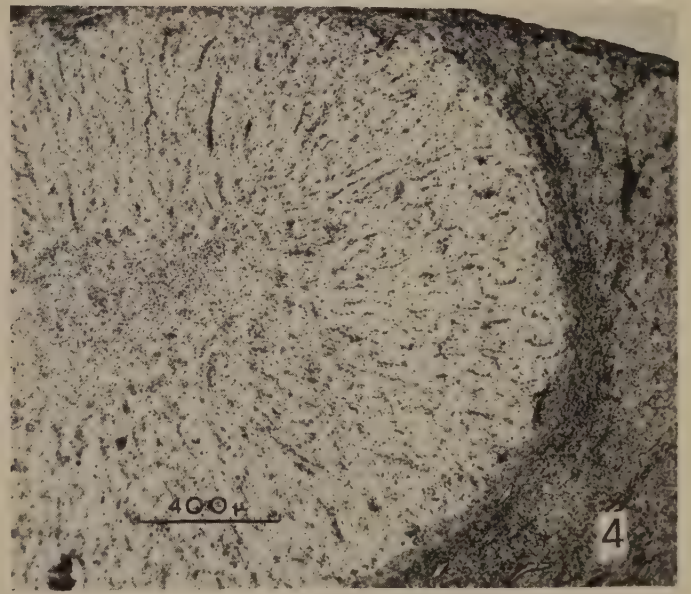
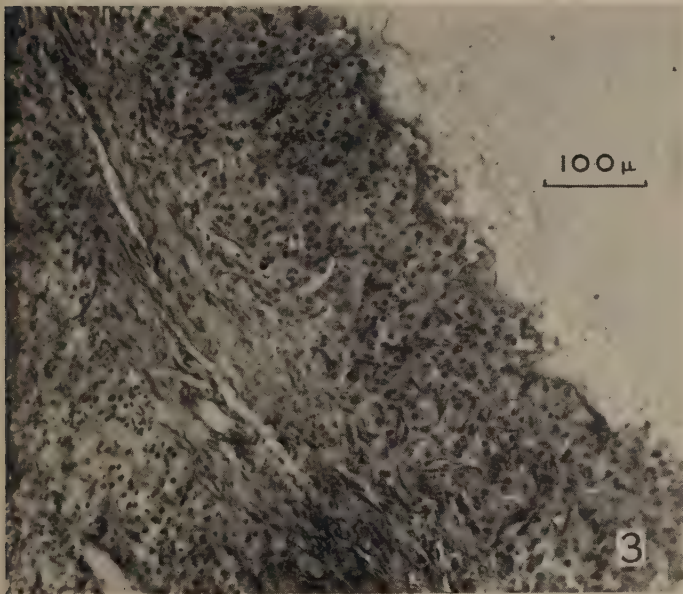
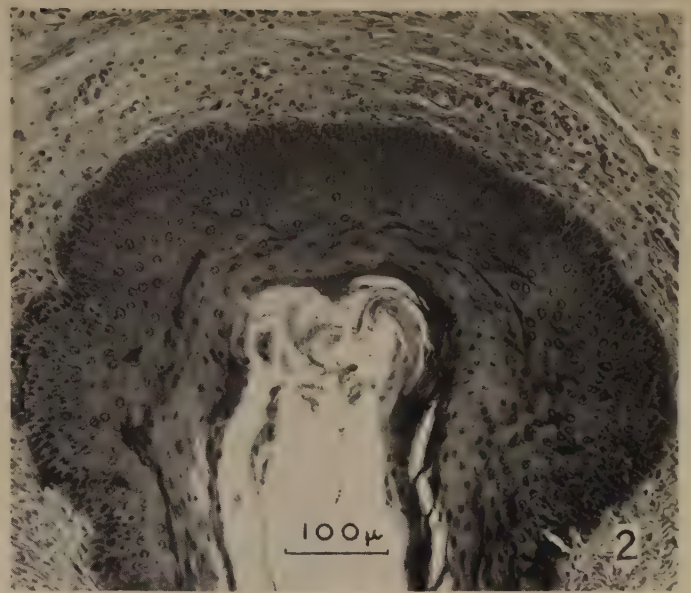
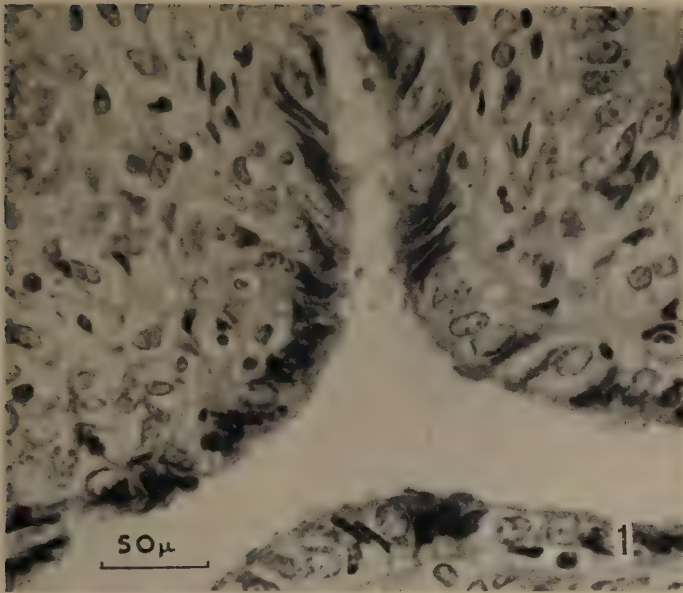


PLATE 3

PLATE 3

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Fig. 2. Photomicrograph of the vaginal epithelium of a young adult killed in April (B.31).

Fig. 3. Photomicrograph of the uterine mucosa of an adult killed in October (B.51).

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Fig. 6. Photomicrograph of the corpus luteum of an adult that had ovulated in September (B.42).

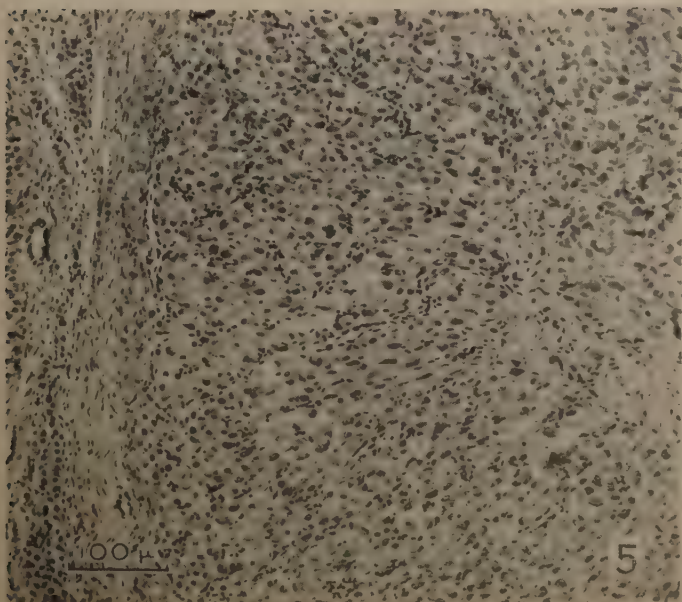
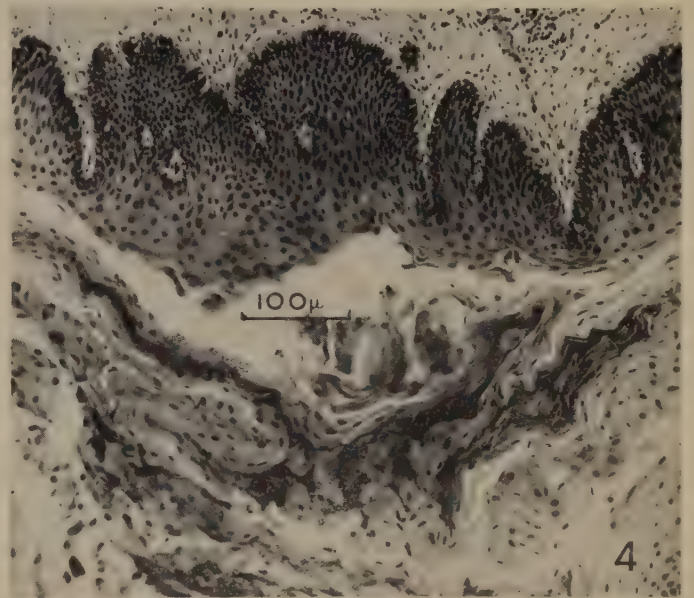
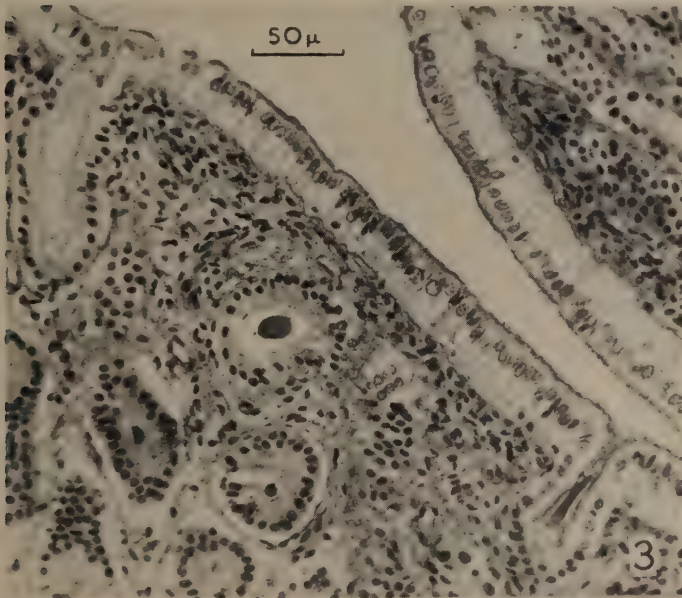
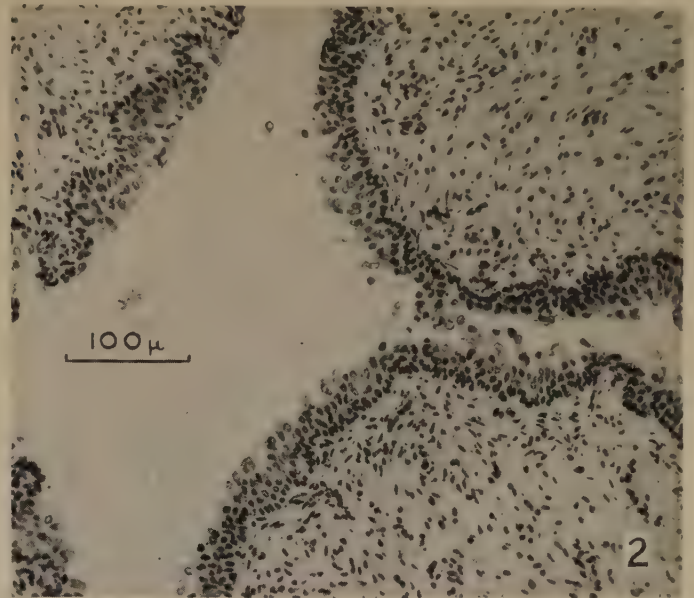
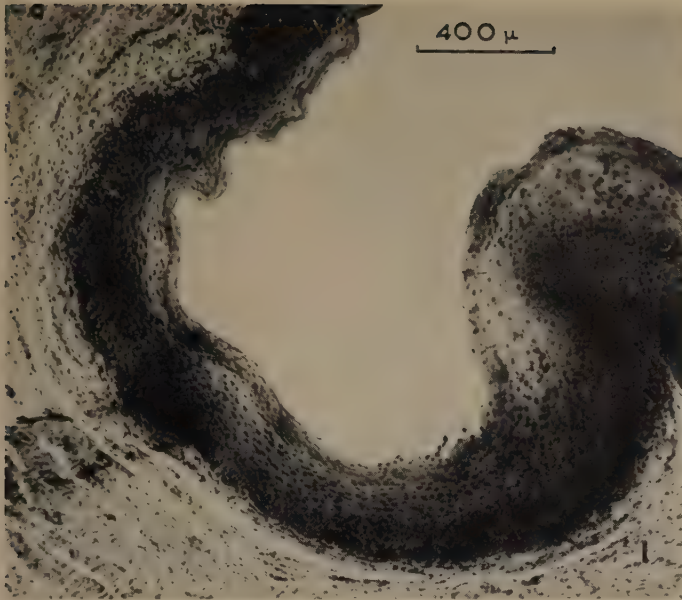


PLATE 4

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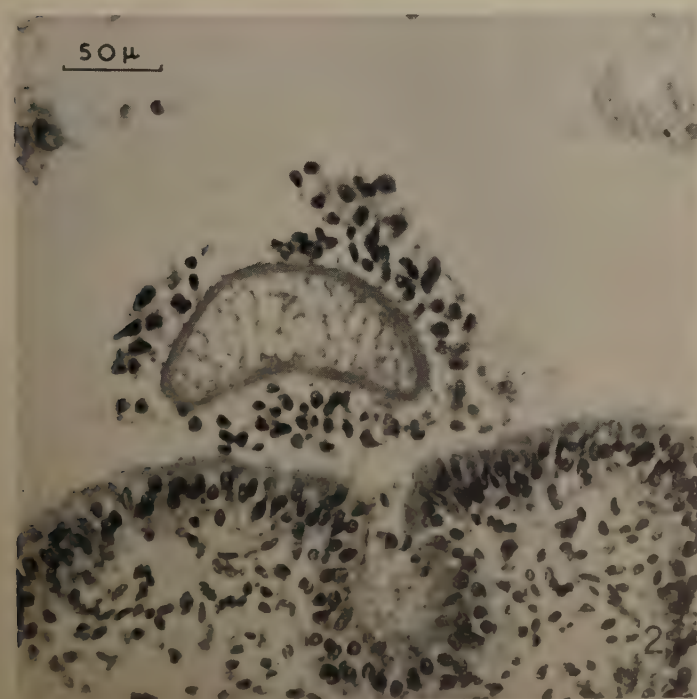
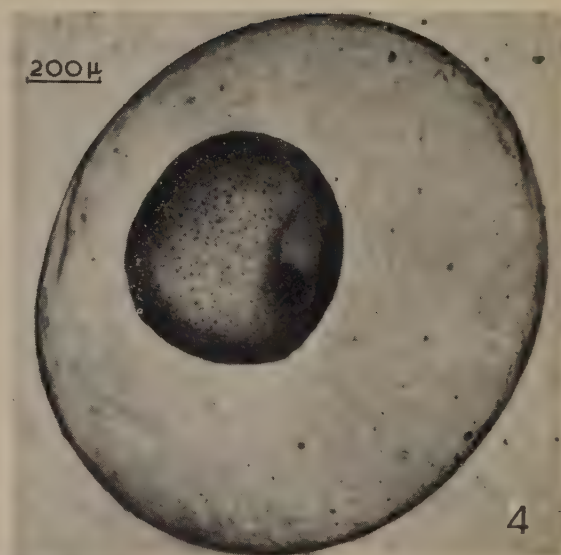
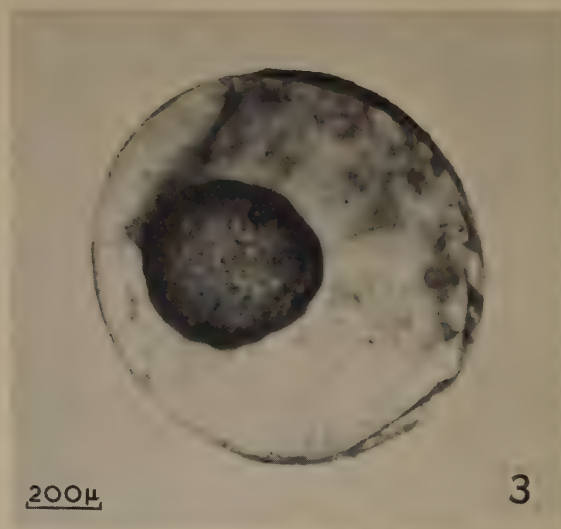
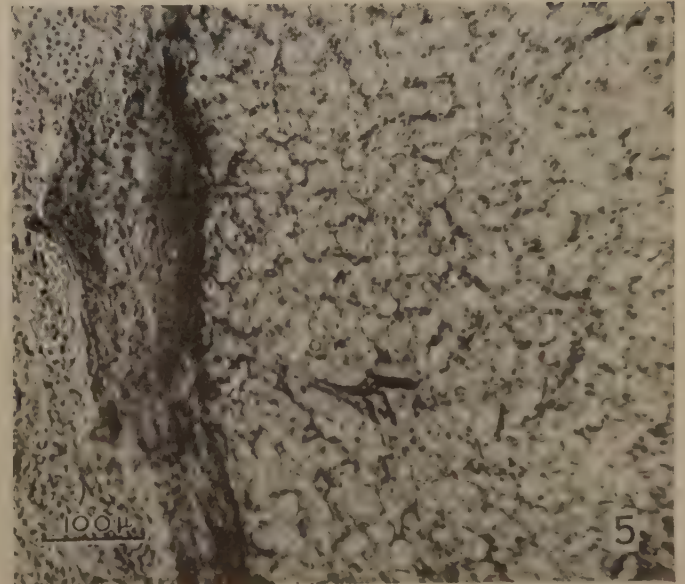
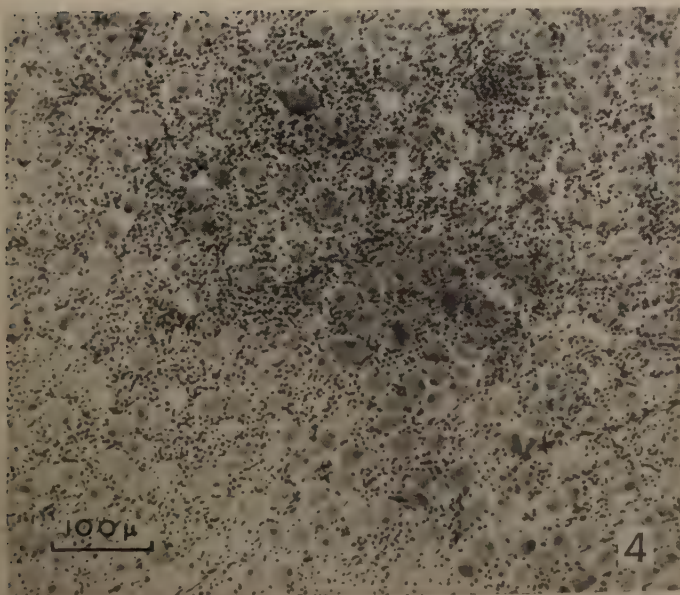
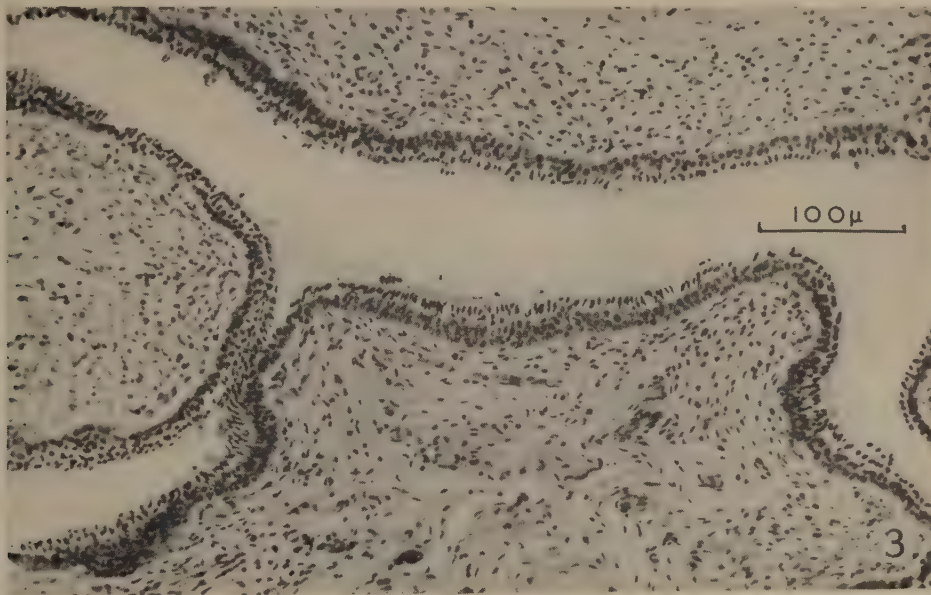
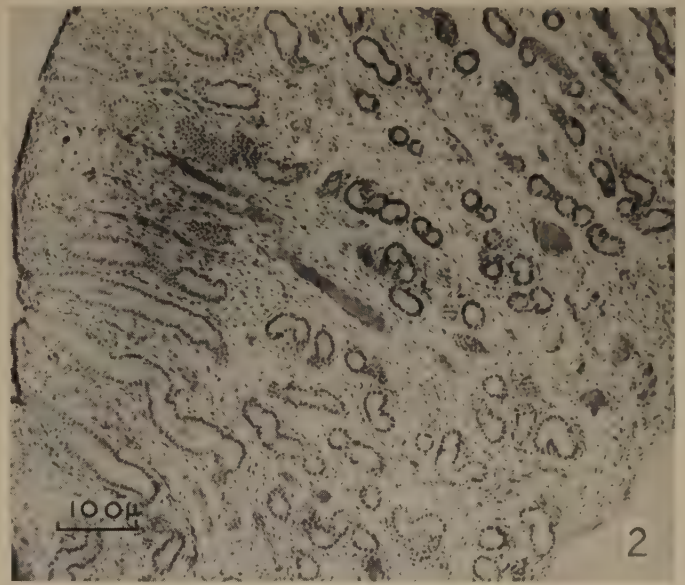
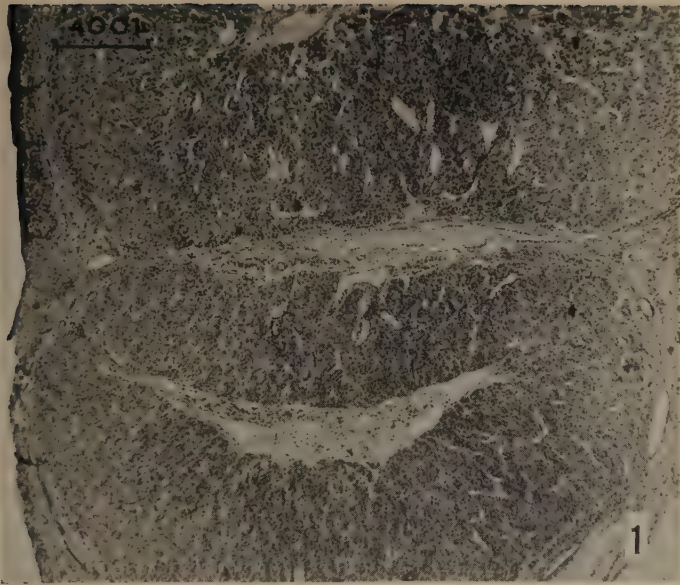


PLATE 5

PLATE 5

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The Anomodont Skeleton

By

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[Accepted 8th March, 1960]

(With 1 plate and 23 figures in the text)

The posterian skeleton of anomodonts is little known, for in contrast to thousands of skulls only some half dozen bodies have been found in South Africa.

Three virtually complete skeletons in the author's collection are therefore described in order to show something of the adaptations presented by the animals, in view of their importance as the herbivorous forms which were the base of a food chain. Of these one is a small endothiodont, the others represent two genera of anomodonts differentiated from *Dicynodon* proper by bodily characters which have implications about the animals' habits.

The paper also includes a survey of food habits of early land vertebrates. One new genus and two new species are founded in it.

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INTRODUCTION

In the Permian rocks of the Karroo of South Africa remains of anomodonts, *Dicynodon* and its allies, are far more numerous than those of any other animal, and the majority of these fossils are isolated skulls, usually with the lower jaw in articulation and the mouth shut. There are at least two hundred South African species described. In addition some four or five species are known from Scotland, some from Russia, and several large Triassic forms from Africa, Asia, and north and south America.

Within the group a series of other genera has been founded, largely on skull structure, beginning with Owen's recognition of *Endothiodon* (1876), greatly added to by Broom, and to a lesser extent by other workers. The smallest skull I know, an *Oudenodon* (R. 315), has a maximum length of 2.9 cm, whilst a skull measuring 79 cm. in length exists, belonging to the Museum of the University of Stellenbosch, and now on loan to Cape Town. Despite this great range in size structural differences of importance are very difficult to find.

It is unusual to find other bones in association with the skull. As Dr Broom—whose experience in that matter was unparalleled—pointed out, complete skeletons of anomodonts, or even smaller groups of associated bones, are extremely rare; perhaps half a dozen postcranial skeletons have been found contrasted with literally thousands of isolated skulls. Thus any postcranial material is worthy of treatment so to increase our knowledge of the anomodonts as to enable us to consider the significance of their abundance, as individuals and as species, within a rather narrow structural group. Broom says, "most of our knowledge of the postcranial skeleton is derived from very small species that have apparently been drowned, and buried in mud under water, and are now shown in a split slab of fine bedded rock," a pond deposit, unlike the bulk of the Karroo sediments. Such specimens show the nature of the carpus and hand, tarsus and foot, excellently, but it is very difficult to discover from them the actual mode of articulation of the limbs, and their possible movements: only separated bones, which can be handled and moved, can give such information adequately. Thus it is difficult to discuss anything of the animals' habits, their food, and locomotion.

The first anomodont to become known was collected by Andrew Geddes Bain, an engineer superintending the construction of military roads in the colony of the Cape. He wrote to the Geological Society of London from Fort Beaufort on 29th April 1844, giving an account of the general geography of the county of Albany from the sea coast to the heads of its rivers. His work is a magnificent introduction to the geology of the Karroo, and led to the discovery of a number of specimens of fossil reptiles, which were sent to the Geological Society by Bain. These were handed on to Richard Owen at the Royal College of Surgeons, who had them prepared and wrote a description of them, illustrated by admirable lithographic drawings, published as an appendix to Bain's account (1845). One was called *Dicynodon lacerticeps*, and is the type species of the genus to which Owen referred two other specimens.

Even in this paper Owen showed that he recognised their general mammalian appearance. He examined the microscopical structure of a dicynodont tusk and

concluded that it more resembled the tissue in carnivorous mammals than in any reptile. He also recognised that in its condition of permanent growth the tusk was mammalian rather than reptilian in character.

Further papers (1855–81) by Owen, who never had a complete skeleton, or even a large part of one, described a number of isolated postcranial bones which he referred, correctly as it now seems, to dicynodonts; unfortunately the pelvis he attributed to that animal (1862) was that of a pareiasaur—but in 1881 he got a dicynodont pelvis, that of *Platypodosaurus*.

This series of papers remained as our only source of knowledge of dicynodonts until Seeley, between 1888 and 1905, described various materials now known to be anomodont, of which *Keirognathus*, a partial skull in association with much of a skeleton, all in bad preservation, made it possible to gain an idea of the animal as a whole. The only point which deserves mention is that he did recognise that the upper end of the scapula inclined forward, though he greatly exaggerated its slope, and he recognised the existence of a clavicle, scapula, pre- and post-coracoid, interclavicle and sternum, all previously recognised by Owen, though not in association with one another. Later (1900) Seeley described *Dicranozygoma*, a considerable part of a dicynodont skeleton, represented by a mould in fine sandstone. This account was the first to give any considerable knowledge of the general structure of the dicynodont skeleton, showing amongst other things the extraordinary length of the ribs in the early dorsal region, and the existence of long free ribs on the last presacral vertebra.

Lydekker (1890) gave an excellent figure of a restored pelvis of a dicynodont.

Newton (1893) described the remains of dicynodonts from Cutties Hillock, Elgin, as *Gordonia* and *Geikia*. This admirable paper not only exploited bones preserved as moulds, but gave the first really easily understandable account of any dicynodont skull.

Broom (1901) gave the first effectively complete account of a skeleton from one he had himself found in the district of Pearston, and called "*Udenodon gracilis*." This was contained in a split slab, a bedded sediment, almost certainly laid down in a small lake. Admirably complete though the skeleton is, giving the structure of the hand and foot in perfection, it does not allow a reconstruction to be drawn. In 1905 he described the structure of endothiodonts, including much of a large form, *Esoterodon angusticeps*, and of another small animal in a split slab, *Chelyoposaurus*, with a good fore limb. He gave (1915b) a photograph (about one-quarter natural size) of a skull, complete vertebral column, and some leg bones of *Dicynodon planus*, from the *Cistecephalus* zone of Kuilspoort, and a similar one of *D. psittacops*. A survey of all Broom's fundamental work on dicynodonts will be found in his independent book, "The mammal-like reptiles of South Africa" (1932).

In 1911 I gave a short account and a restoration of the skeleton of *Lystrosaurus* whose hand and foot were incomplete. In 1917 I figured a shoulder girdle and fore limb of *Dicynodon halli*, with drawings by Miss Woodward of the bones actually set up in natural position.

In 1924 Helga Pearson gave an admirable account and reconstruction of the large, late and unusual dicynodont *Kannemeyeria*.

Von Huene (1931) obtained from his collector a partial skeleton of a small individual of *Dicynodon testudirostris* Broom and Haughton, with a skull, fore and hind limbs, but no vertebral column, and also a larger skeleton, *D. kolbei*? Br., with an incomplete skull, vertebral column complete up to the root of the tail, many ribs, and the greater part of the limbs (excluding the feet), of which he gives measurements and some figures. Von Huene has published a map of the Karroo showing the distribution of the zones and of many localities, which is most useful.

In 1937 Broili & Schroeder described as *Dicynodon broomi* material from the Tapinocephalus zone which seems to provide a good example of the occurrence of toothed and toothless forms, presumably male and female respectively, of the same species.

The problem presented by the existence of a very large number of skulls all referred to the genus *Dicynodon* has been considered by Toerien (1953), who has begun to split up the great group on the stage of evolution of the palate.

Finally, an admirable skeleton of a dicynodont from the Cistecephalus zone of East Africa has been described as *Kingoria* by Cox (1959). It is somewhat unusual in structure but in the main it is good dicynodont.

LIST OF MATERIAL

I now have in my own collection three specimens, each of which shows most of an anomodont skeleton.

(1) *Diaelurodon whaitsi* Broom,* R. 451, from the Lower Endothiodon zone, Hans Rivier Dam, Beaufort West Commonage, Cape Province, is the oldest. It consists of an articulated skull and lower jaw, essentially complete and well preserved though slightly distorted by pressure. The axis and fragments of the atlas are in position, and the vertebral column is in articulation to the twelfth vertebra. This group of vertebrae includes the primary shoulder girdle of each side apparently in natural position, part of a clavicle, and a humerus in articulation; the other humerus, lacking a little of the middle of the shaft but otherwise well preserved, is in articulation with a forearm, carpus and nearly complete hand. Where the vertebral column is broken through, an isolated vertebra, the thirteenth, lies upon a perfectly preserved sternum. Then follows a well preserved stretch of vertebrae which extends back until, at the twenty-ninth, it is in articulation with the sacrum, behind which are some rather displaced caudal vertebrae. The pelvis is in position, essentially complete. The hind leg is represented by a femur of known length (lacking the middle of the shaft), and parts of a tibia and fibula, together with a tarsus. The matrix responds well to acetic acid, and

*Toerien (1953) has revised the small endothiodonts of the Tapinocephalus and Endothiodont zones, concluding that *Pristerodon mackayi*, the first described species, which comes from East London, is characterised by the possession of teeth which bear denticulations on both anterior and posterior edges. He refers Broom's *Diaelurodon* to *Pristerodon* on the ground that it is extremely like *P. buffaloensis*, the type of the genus. The specimen which I have described and referred to *D. whaitsi* shows the upper post-canine teeth etched out from the matrix, and the three which are visible lack denticulations along both front and hinder edges, but this may be due to condition. Apart from the lack of serrated teeth the specimen is so like Broom's type (A.M.N.H. 5507) that I regard it as the same thing. They were found at the same horizon, and in all probability within a few yards of one another.

much of the bone surface is shown in perfection. The skull is 8.3 cm. long, and the whole animal to the root of the tail measures 38 cm.

(2) *Diictodon sesoma* sp. nov., R. 314, ? Upper Endothiodon zone or Cistecephalus zone. I found this specimen—the last I collected in 1949—in blue/grey mudstones immediately south of a low bridge crossing the Buffels River, on the main road from Murraysburg to Nelspoort, O.F.S., as I was on my way back to England. This locality is remarkable because over a considerable area of river bed, exposed where there is a small waterfall, the mudstone is richly speckled with white bone, not restricted to any one bedding plane, and evidently laid down in some unusual way, perhaps as a result of flood. R. 315 came from the same place. The specimen consists of an articulated skull and lower jaw. An articulated series of some eighteen vertebrae from the sacrum forward. The complete sacrum of three vertebrae, and about five caudal vertebrae. The pelvis—in position—and both hind legs preserved in part, a few digits of one hind foot being present. The well preserved shoulder girdle, and a fore limb complete to its claws. There is also a series of five anterior vertebrae. The skull length, nose to occipital condyle, is 8 cm. The matrix does not respond well to acid, is very hard in places, and is difficult to prepare with a chisel.

(3) *Diictodontoides skaios* gen. et sp. nov., R. 396, from the Cistecephalus zone, hillside on Commonage, 4 miles north of Murraysburg, Cape Province, collected by Mr. James Kitchin. The specimen comprises a skull and lower jaw in articulation, lying right side down on the well preserved right hand. The first seven vertebrae, in articulation, lie far removed from the skull between the pelvis and the left hind leg. Four articulated vertebrae, lying some distance behind the skull, though nearer to it than the length of the neck, are separated by a gap from a dorsal vertebra, probably the nineteenth, from which a continuous series curls round to the sacrum of three vertebrae. The shoulder girdle, thrown somewhat out of position, is well shown, and one complete fore limb is present, parts of the other are preserved in matrix detached from the main block. The ilia lie nearly in position one on each side of the sacrum. The pubis and ischium of the right side are in position but a little twisted, whilst on the left they have been moved for some centimetres but are beautifully displayed from the outer surface. Each femur is nearly in articulation with the pelvis, and the lower leg, some tarsals, and a hind foot are well preserved. Enough ribs remain to give some idea of their character. I prepared this specimen, which hardly responds to acid, from a grey matrix which is a typical example of wind blown dust, since it fractures unexpectedly in cubical lumps. The skull is 9.6 cm. long, and the animal as a whole about 47 cm. in length.

As well as these three specimens I have available the following material from my collection:—

R.53, *Dicynodon cf sollasi* ♀, Upper Endothiodon zone, Kuilspoort Nek, near Beaufort West, C.P. A complete skull 10 cm. in length (figd. *Proc. zool. Soc. London* 118), with atlas and axis, also a hand (R.30).

R.235, large dicynodont axis, Cistecephalus zone, "Schneuberg," perfectly preserved, given me by S. H. Rubidge, prepared with acetic acid.

R.237, *Dicynodon* sp., Cistecephalus zone, "Schneuberg," a skull, the smallest uncrushed specimen.

R.262, *Dicynodon* sp., Cistecephalus zone, "Schneuberg," anterior part of a skull of medium size, important because, as the lower jaw is not in position, it has been possible to prepare the canine teeth so as to show the nature of the wear facet made by the beak of the lower jaw on their inner surface.

R.264, *Dicynodon* sp., Cistecephalus zone, "Schneuberg," small skull with tusks showing no wear facets.

R.265, *Oudenodon* sp., Cistecephalus zone, "Schneuberg," anterior part of a small skull showing a magnificent palate, exceptionally well exposed in a mechanical preparation.

R.276, "*Dicynodon*" sp., Cistecephalus zone, Thabanchu, O.F.S., posterior part of a very large skull, nearly complete right scapula, part of ischium, neural arch, etc.

R.280, right humerus of a large dicynodont, Cistecephalus zone, Thabanchu, O.F.S., remarkable because it is perforated by a hole, about a centimetre across, full of small bone fragments, which is presumably the result of a bite.

R.301, perfect isolated dicynodont sternum of large size, Cistecephalus zone, "Schneuberg," prepared by acid.

R.302, *Dicynodon* sp., Cistecephalus zone, "Schneuberg," incomplete skull, 6 cm. in length, prepared with acid and showing a vestigial tooth.

R.311, a and b, *Dicynodon* sp., Cistecephalus zone, "Schneuberg," occiput (a) and atlas (b), in articulation, of a very large skull 30 cm. across the quadrates.

R.315, *Oudenodon* sp., ? Cistecephalus zone, Buffels River, on main road from Murraysburg to Nelspoort, O.F.S., at a low bridge. This skull (found with R.314), weathered on the right side, is well preserved and complete from the occiput up to the cast of the inner surface of the internarial process. The lower jaw is in position, the mouth a little open. The dentaries are not fused and meet in a suture. The sphenethmoid is misplaced into the left orbit, and three sclerotic plates are present there. The total length is 2.9 cm. and it is the smallest dicynodont skull I have ever seen; it is probably infantile. Two vertebral centra, a series of ribs, parts of the shoulder girdle, a humerus, and the head of a femur are also preserved.

R.321, footprint slab, base of the Lystrosaurus zone, Middelburg, C.P., with a track of six reptilian footprints.

R.443, *Dicynodon pygmaeus*, Broom and Haughton, Lower Endothiodon zone, Hans Rivier Dam, Commonage, Beaufort West, C.P. The skull, length about 5.6 cm., is interesting because the upper canine tusk on the left side

is still in the alveolus, not yet cut. There is a series of about a dozen vertebrae behind it, with half a shoulder girdle and a humerus attached. The specimen gives direct evidence of the character of a juvenile, and of the existence of a neck. Partly exposed by acetic acid.

R.491, anomodont scapula, Cynognathus zone, Lady Frere, O.F.S.

R.497, a large undeterminable dicynodont from the top of the Endothiodon, or bottom of the Lower Cistecephalus zone, summit of Nieuvelde Escarpment, found by a farmer in the region where the road from Prince Albert Station to Fraserburgh, District Albert, C.P. crosses the escarpment. It is represented by a series of eighteen articulated vertebrae, with some rib heads in articulation, the hinder end of one ramus of the lower jaw, the lower end of a femur, tibiae, radius and ulna. There are also three additional vertebrae (R.523), and part of the occiput, and other skull fragments (R.522). The chief importance of this specimen is that it is large. The complete presacral vertebral column must have been over 76 cm. long, and the skull perhaps 40 cm. wide: it is, perhaps, two-thirds the size of such a form as *D. leoniceps* or *D. tigriiceps*, both figured (natural size) by Owen (1855). The bone is badly cracked and weathered and can be prepared with acetic acid to a limited extent only.

R.498, coracoid, precoracoid, and glenoid end of scapula of an immense dicynodont given me by S. H. Rubidge, well preserved and now free from matrix. The skull must have been some 80 cm. in length. Cistecephalus zone, Hoekplas, District Murraysburg, C.P.

R.514, *Dicynodon* sp., non. loc. Anterior part of a small skull and lower jaw etched out with acetic acid to show, in perfect preservation, floor of air passages.

R.516, *Dicynodon* sp., Cistecephalus zone, hillside on Commonage, Murraysburg. Small skull.

R.519, *Dicynodon bolorhinoides* sp. nov., Upper Endothiodon zone (or Lower Cistecephalus zone), Kuilspoort, near Beaufort West, C.P. This large skull 27.5 cm. long, with lower jaw in articulation, was collected from the mudstones towards the base of the hill at Kuilspoort. It is unusual in not being surrounded by a nodule, and it was unnecessary to prepare it with a hammer and chisel, as frost and other natural causes had so broken up both matrix and bone that it shows many internal morphological features, and details of tooth wear, etc., very well.

I have also had available the following specimens from the British Museum (Natural History):—

B.M.N.H. R.4067, *Dicynodon halli*, type specimen, Lower part of the Cistecephalus zone (or possibly Upper Endothiodon zone) of Kuilspoort, near Beaufort West, C.P. This specimen I found on a very steep hill slope, behind and much above the house of Kuilspoort. It consists of a perfect skull and articulated lower jaw, an axis not completely *in situ*, a few dorsal vertebrae, a splendid sacrum with some caudal vertebrae, fore and hind limb girdles and limb bones, a few rib fragments, and parts of a hand or foot.

B.M.N.H. R.3747, a beautifully preserved dicynodont neck and anterior part of the vertebral column, with a humerus in association. Seeley Collection, "Near Nieuveltdt," C.P.

B.M.N.H. P.6922, *Tropidostoma microtrema*, Bain Collection (see footnote on page 159). Part of the pectoral region including the lower end of the right scapula, with the coracoid and precoracoid, the lower half of the right clavicle, the interclavicle and sternum in natural articulation, with a series of vertebrae attached to their upper surface, similar in size to *D. halli*.

B.M.N.H. P.6923, *Tropidostoma microtrema*, Bain Collection. The lower end of a right scapula with a clavicle in articulation, resting on a series of vertebrae and ribs, and the upper part of a humerus.

B.M.N.H. P.6924, *Tropidostoma microtrema*, Bain Collection, Right pelvis, including ilium, pubis and ischium.

B.M.N.H. P.6925–P.6954, thirty snouts of *T. microtrema*, Bain Collection, of which P.6925–35 are measurable.

DETERMINATION OF COMPLETE SPECIMENS: *Diaelurodon whaitsi* BROOM, *Diictodon sesoma* SP. NOV., *Diictodontoides skaios* GEN. ET. SP. NOV.

I propose to describe, and especially to compare with one another, those anomodonts available to me which are represented by considerable parts of skeletons, so that it is possible to gain a clear idea of their general structure, and thus of their mode of life.

There are two problems involved—the actual fundamental group structure, and the range of variation within it. The work is based essentially on my three more or less complete small skeletons, compared with the partial but well preserved type specimen of *D. halli*, and with the many small groups of isolated bones listed above.

The skull of *Dicynodon* has been described repeatedly, and is well known. In the present paper it is only dealt with where my specimens add materially to our knowledge and understanding of its structure, or afford some evidence of peculiar food habits, or to enable the specimens to be determined specifically.

The determination of skulls can only be carried out by a direct comparison of the specimen with the type, or with a figure of it. But before this is possible in anomodonts an approximate determination must be made. The first stage is to discover whether the skull bears any teeth, other than the canines: this should be easy, but is not, for the great majority of dicynodonts are preserved with the lower jaw in position and the mouth closed, and in many cases this condition makes it exceedingly difficult to look for teeth. If such be the case, fractures are more likely than intentional development to show them. If palatal teeth are visible determination is comparatively easy. Broom's "Mammal-like reptiles of South Africa" (1932) gives a list and figures of nearly all those which were known up to the date of its publication. At that time ninety-five species

of *Dicynodon*, and of animals which on first inspection might be referred to that genus, had been described, and the majority of them figured. No one has yet succeeded in producing a scheme by which this genus could be broken up into recognisable and more convenient sections. Toerien, working on palates (1953), has made an interesting beginning, but a great deal of the material is not capable of classification on his lines because of its condition.

Thus, in practice, unless palatal teeth can be found, all that can be done is to compare the skull under consideration with all the figures of such things in Broom's book, and also in the independent papers of Broom, Broom and Robinson, von Huene, Broili, Haughton, Brink, Boonstra, van Hoepen, Kitching, and others. This is a lengthy process, but will only be improved when much further material is properly prepared and described.

Of the three skeletons with which the present paper deals, one, *Diaelurodon whaitsi*, is easily determined: the other two are not.

Diaelurodon whaitsi Broom, R.451, Lower Endothiodon zone, Hans Rivier Dam, Beaufort West Commonage, C.P. (See footnote on p. 135). Comparison of Fig. 1, with Broom's original figure and description (*Proc. zool. Soc. London*, 1911, Pl. 63), which was the basis of the identification, seems to make it quite certain, especially as the two skulls came from almost the same spot. The orbits are widely separated by the frontals, whose width is only a little less than that across the temporal roof. The temporal fossae are long. The occiput is obliquely placed, wide in comparison with its height, and the level of the quadrate condyle is very much below the floor of the brain case. There is fragmentary evidence that sclerotic plates were present. The lower jaw is unusual in two ways: the post-articular process is exceptionally deep vertically, projecting very noticeably below the level of the lower border of the jaw immediately in front of it; and the reflected lamina of the angular spreads out into a very considerable expansion, hanging down below the border of the mandible, as shown in the figure. The upper teeth, considerably worn, can be seen on the left side of the skull. The posterior two are firmly planted in the maxilla, the tooth immediately in front of them has fallen from its socket and shows a large pulp cavity with an open root. Further forward, so that it lies mesial of the canine tusk is another tooth. The upper teeth show no signs of serration. The mandibular teeth are seen only in an oblique section which shows five teeth graded in size, the largest being posteriorly. The implication is that they are very like the upper teeth and conform to a reduced endothiodont pattern. This specimen shows very clearly an open suture between the right and left dentaries. The apparently fused splenials remain in natural articulation with the left dentary, but have parted from the right, which has moved away from them for a distance of a little more than a millimetre. The premaxillae of the specimen also show, especially in palatal view, an open suture between them; although very seldom seen both conditions imply youth.

This specimen is remarkable because at the back of the left orbit there is an oval mass of matrix (diameter 7 mm.) which has a sharply defined limit, the matrix within it differing very much from that surrounding it. It passes back-

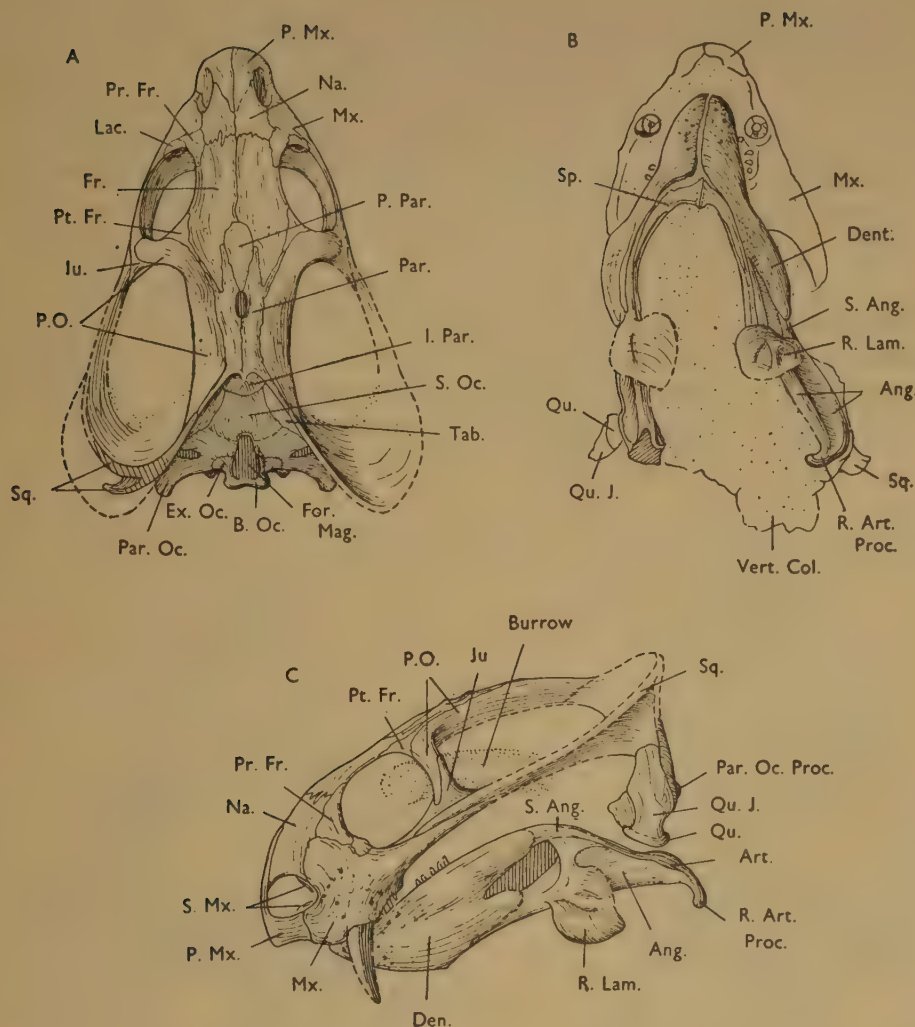


Fig. 1. *Diacelurodon whaitsi* Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P. $\times \frac{2}{3}$.

A, restoration of the skull from above, outline of the squamosals restored. The left squamosal is incomplete and shows the occipital plate separated from the body of the bone by a notch; B, the specimen *in situ*, seen from below, showing the distribution of the upper teeth, the open suture between the dentaries, and the position and character of the reflected laminae of the lower jaw. The matrix projecting posteriorly contains the first three cervical vertebrae, displaced laterally from the condyle; C, restoration of the lateral surface of the skull, the teeth in the lower jaw being restored on the evidence of those seen in section in the left dentary. The reflected lamina of the left side is well shown in the specimen, though some parts of its outer surface have weathered away. The dotted structure in the orbit and temporal fossa represents the distribution of the insect burrow mentioned on p. 140. The large foramina which are associated with the development of the horny beak are well shown on the maxilla and the dentaries in B and C. R. Lam. indicates the reflected lamina of dicynodonts, here exceptionally well developed. Burrow, insect burrow; (key to abbreviations p. 206).

wards and inwards into the temporal region for a distance of at least 35 mm. and extends to within a very short distance of the front surface of the occipital plate. It is evident that its existence is not determined by any feature of the reptile structure, and the only explanation I can give is that it represents the burrow of an insect, or spider, made in the earth filling the skull at a time when it lay near to the surface of the ground, and presumably by pure accident was filled up with blown dust of a different character from the surrounding soil, and so preserved.

Diictodon sesoma sp. nov., R.314, ? Upper Endothiodon, or Cistecephalus zone, Buffels River, O.F.S. is remarkable in that the pineal foramen is completely surrounded by the preparietal (prepineal). This condition has previously been found only in the skull which Broom (1913) described as *Diictodon galeops*. But

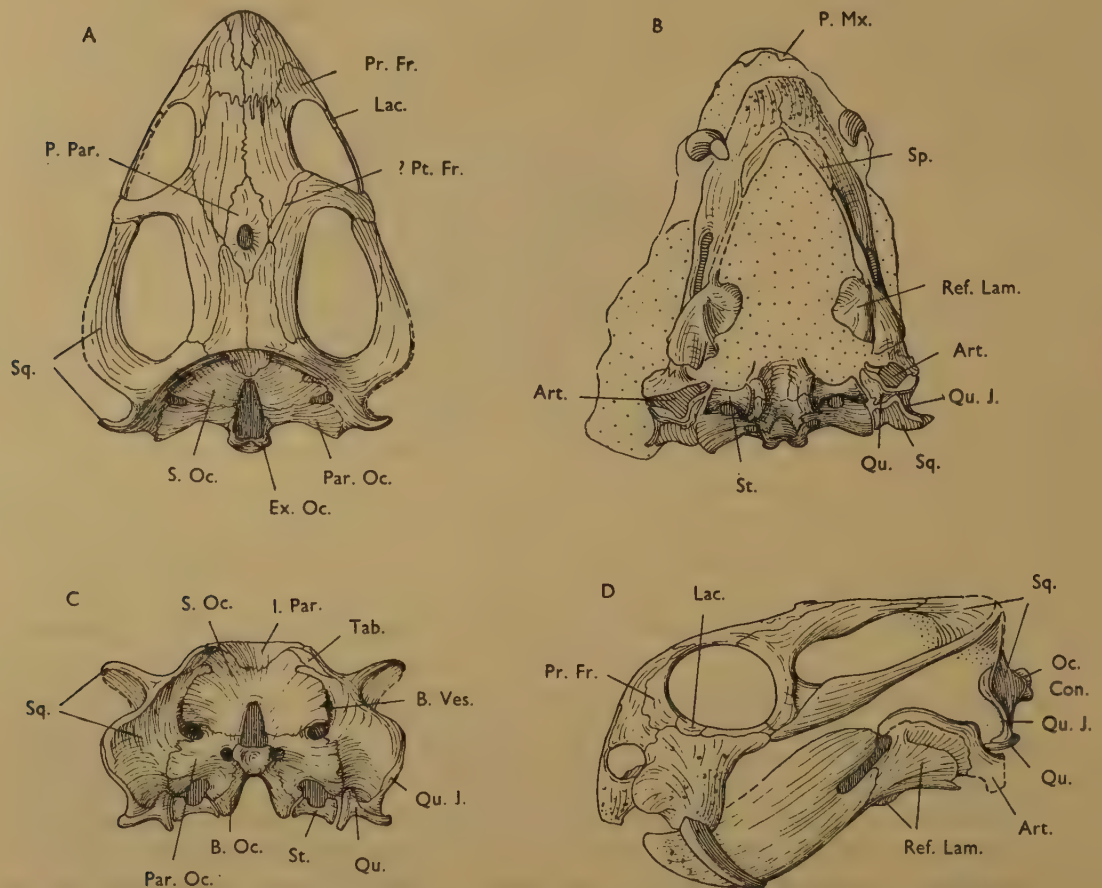


Fig. 2. *Diictodon sesoma*, sp. nov., R.314, ? Upper Endothiodon zone, Buffels River, O.F.S. $\times \frac{3}{2}$. A, restoration of the skull from above; B, the skull *in situ* from below, the cross hatched areas on the articulars are fractures; C, restoration of the occiput, the lower jaw is not represented because the descending processes of the articulars are broken off, so that they are scarcely visible; D, restoration of the left lateral surface.

B.Ves., groove for the blood vessel referred to on p. 143. (Key to abbreviations p. 206).

it is evident that the present specimen is not *D. galeops*, being shorter and broader, with a much wider occiput, and a relatively wider intertemporal region. In side view the canine is much larger than in the type of the genus and the maxilla round its base is much deeper. I call it *Diictodon sesoma* because it has a body preserved. The essential qualities are most readily determined from Fig. 2. A small slip of bone on the right appears to be an independent postfrontal, but this bone is not shown on the left, and the apparent suture on the right may be only a crack. The gutter (B. Ves.) extending up between the squamosal and supraoccipital from the outer end of the post-temporal fossa is a remarkable condition, which can imply that the neck muscles and other structures of the back of the skull drained blood into the great head vein which comes out through the fossa. In general shape the skull is unlike most other dicynodonts, the complete enclosure of the pineal foramen in the preparietal is at present quite characteristic, and another specimen should be capable of recognition from the figure.

Diictodontoides skaioi, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P. has a good, but somewhat laterally compressed skull, represented in Fig. 3.

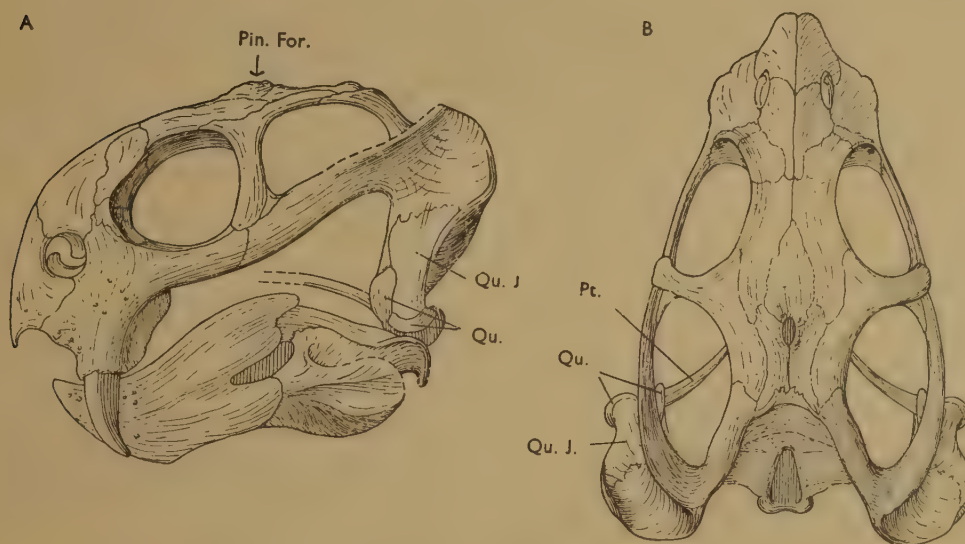


Fig. 3. *Diictodontoides skaioi*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P. x $\frac{2}{3}$. Restoration of the skull, A, left lateral view; B, dorsal aspect; note the absence of a post-frontal. (Key to abbreviations p. 206).

It does not agree with any specimen yet figured, and should be regarded as new generically as well as specifically. To it I give the name *Diictodontoides skaioi*—*Diictodontoides* to imply that the skull is very like that of *Diictodon galeops*, as figured by Broom, though it differs definitely in that the pineal foramen is not completely surrounded by the preparietal as it is in that form, *skaioi* implying that the animal is of clumsy build. The skull is characterised by being very high in proportion to its width and length. The temporal fossa, not much larger than

the orbit, extends far backwards. The squamosal projects well behind the occipital condyle, and its descending ramus flares outwards and a little forwards ending just above the quadrate condyle, the quadratojugal being welded onto a great deal of its anterior face. The orbit is large, the face in front of it short, with a powerful descending maxillary process in which the short but massive canine is inserted. The premaxilla is short and the nostril high in the skull. The lower jaw has a large reflected lamina projecting downwards and turned a little inwards.

OBSERVATIONS ON DICYNODONT SKULLS

Nutrient foramina

The three dicynodont skulls of *Diaelurodon*, *Diitcodon* and *Diictodontoides* are unusual in that they show, very well preserved and obvious, a series of foramina coming out onto the surface of both upper and lower jaws. These appear on the lower part of the premaxilla, where they are abundant; on the lower border of the maxilla, and round the root of the canine tusk, implying that it projects from the gum internal to the surface of the head; and over the anterior end of the dentaries; and they exist in toothless forms (*Oudenodon*) as well as in *Dicynodon* proper. The foramina lead into long, narrow canals of rather constant diameter, and open straight onto the surface by their full diameter. They can be matched with similar openings in chelonian skulls, which are nutrient foramina associated with the development of the horny beak, and they no doubt have the same function in dicynodonts, where they give some indication of the extent to which that structure was developed. It evidently formed a sharp-edged ridge round the margin of the jaws, covered something of the palate, and ended so soon as to suggest that the beak was short in both jaws.

One oudenodont snout (R.265) (Fig. 4A) shows in perfection the outer surface of the premaxilla and some of the maxilla, naturally weathered, and the anterior part of the palate, in a very successful preparation. The existence of a horny beak in *Dicynodon* was recognised by Owen and has never since been disputed, but this specimen is remarkable in that it adds noticeably to our understanding of the extent to which it spread, the Chelonia—which provide such a clear parallel—affording confirmatory evidence as to the validity of the criteria used.

Vestigial tooth

An undeterminable dicynodont skull, 6 cm. in length, R.302, (Fig. 4B), is of interest because it shows not only a very well preserved palate (which confirms the rich development of nutrient foramina in those regions of the premaxilla and maxilla which were covered by a horny beak) but also the occurrence in the right maxilla of a rudimentary tooth, whose tip is just seen through a well finished opening in the maxilla immediately internal to the damaged ventral process normally found round the root of the canine. This vestigial tooth, visible on one side of the jaw only, is presumably the remnant of the canine. Behind it the maxilla is produced into a very short, blunt, downwardly directed process (Boss),

entered from behind by a foramen, or two or three foramina, presumably for blood vessels. This structure, which I have not seen in any other specimen, probably has some relation to the beak.

Maxillary antrum

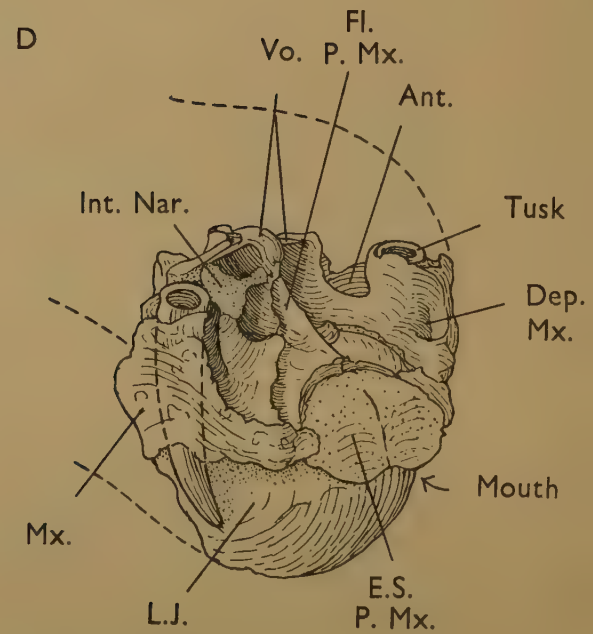
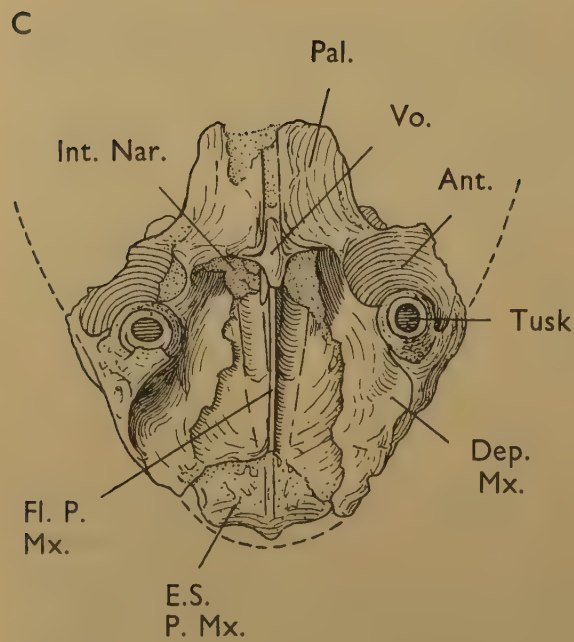
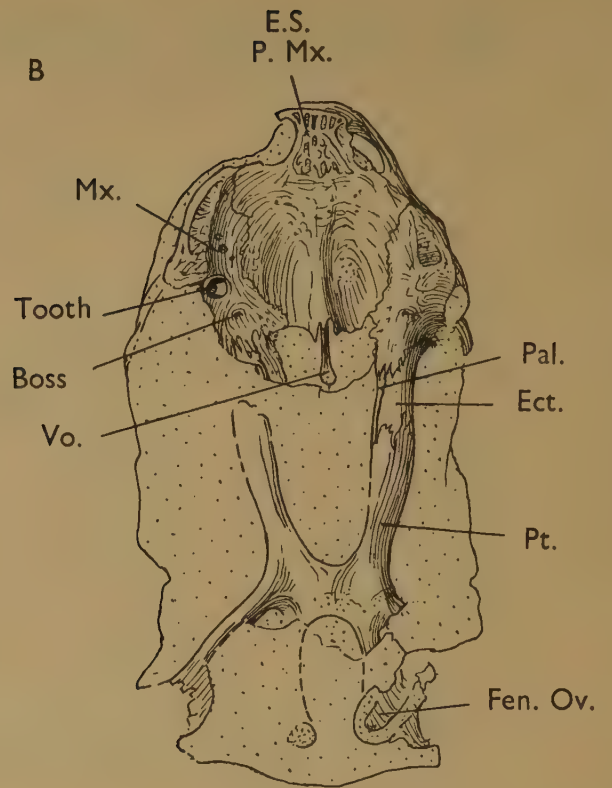
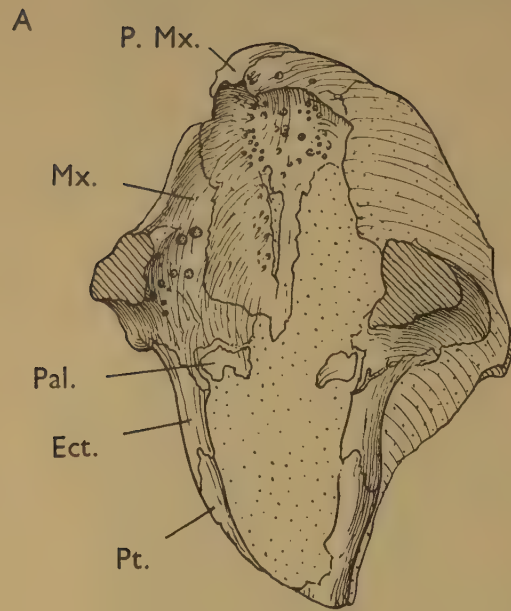
A small fragment of dicynodont muzzle, R.514 (Fig. 4C & D) has been prepared with acid so that it shows, from above, the floor of the nasal passages from the external to the internal nostrils. The premaxillae, perfectly shown, bear a median ridge, anteriorly low, which rises as an extremely thin, deep plate (Fl.P.Mx.) as it passes back to the internal nostrils. Anteriorly, in front of the root of the canine tooth, there is a rounded depression (Dep.Mx.) on the floor of the cavity which forms a lateral expansion of it. The internal nostrils are narrow but very deep, separated from one another by the extremely thin median septum of the premaxillae, which is clasped between equally thin flanges of the vomers, which fuse with one another above to cap it. The roof of these passages is formed by the palatines, and they become shallower as they are traced backward. Their outer walls are made by the maxillae which extend back until they are overlapped by the ectopterygoid (or transverse) bones (not visible in the drawings). There is a maxillary antrum lying behind, and even lateral to, the bony socket sheathing the root of the canine, and this (which was clearly filled with air) opens into the lateral wall of the main air passage immediately outside, but much above, the actual internal nostril.

Reflected lamina

The reflected lamina of the angular bone of the lower jaw is a structure found in all therapsids from sphenacodont pelycosaurs onwards. Its function is still unknown, although its appearance is familiar, since it is shown in very many specimens. Not only is the existence of the lamina known, with the pocket behind it, but it is evident that it must have been of some real significance in the life of the animal, or it would have been most unlikely to have been preserved by every individual in the whole group, whatever its age, size, general build and habits.

The general nature of its variation in character is rather well shown in the specimens of anomodonts figured here (Figs. 1, 2, 3, etc.). The conditions in *Diaelurodon*, *Diictodon* and *Diictodontoides* differ sufficiently *inter se* to suggest that the structure was functional in the sense that it provided a cavity in which some organ of importance, which had to be protected from pressure, lay. What this organ was is extremely difficult to determine.

In *Diaelurodon* the swollen flange of the lamina, extremely thin-walled, is none the less very large, extending down a considerable distance below the main part of the angular, and it could—indeed it must—have housed a very considerable structure lying dependent from the ventral border of the lower jaw, and extending up the lateral surface of the hinder part of the jaw nearly to its articulation with the quadrate, though cut off from it by the ridge of the upper border of the surangular. In *Diictodon* there is again a large space between the reflected lamina



[See facing page]

and the admesial surface of the lower jaw, which it surrounds, passing inward towards the middle line and forming, as it were, a floor between the rami of the lower jaw. In *Diictodontoides* the reflected lamina is a deep structure swollen out well away from the body of the lower jaw, and extending down it for some way. Even in the smallest known dicynodont (R.315) the reflected lamina is well preserved on both sides of the head, and that a pocket exists between it and the rest of the outer surface of the hinder end of the jaw is most beautifully shown, together with the fact that the lamina descends well below the lower border of the jaw; so that here also the pocket may be assumed to have housed a structure which extended downward below and indeed inwards mesial of the lower surface.

This reflected lamina is restricted to the mammal-like reptiles, first appearing among the pelycosaurs, (in *Dimetrodon* and *Secodontosaurus* only). It varies considerably in extent; in *Dimetrodon* it is merely a notch in the lower border of the exceedingly deep angular, with a pocket behind it. From sphenacodonts it was carried into therapsids; it is found in all deinocephalians, anomodonts, gorgonopsids, cynodonts and dromosaurs. In the advanced cynodonts like *Diademodon* it is a free, slender and quite long process extending backwards from its origin on the angular, and its last appearance is as the slender, elongated process in the cynodont *Protacmon*. It survives, in effect, in the tympanic of mammals.

In 1948 I suggested that the lamina lay external to a sheet of tendon which

Fig. 4. Fragments of three anomodont skulls, all $\times 1\frac{1}{2}$.

A, small ouidenodon, R.265, Cistecephalus zone, "Schneuberg," showing the perfectly preserved right half of the palate in oblique view. The great development of the fused premaxillae is exceedingly well shown, and the small exposure of the palatine is shown on both sides. The important features are the series of nutrient foramina in the premaxilla and maxilla: it seems evident that these exist for the formation of the horny beak and thus give an indication of the area covered by that structure. B, acid preparation of a small dicynodont palate, R.302, Cistecephalus zone, "Schneuberg." This is damaged peripherally but the main surface is beautifully shown. The most interesting features are:—(i) the nutrient foramina for the beak, seen in advance of the right canine tusk, and the existence posteriorly in the maxilla of a well defined boss, entered from behind by a foramen, which must play its part in the attachment of the hinder end of the beak; (ii) the great expansion of the premaxillae on the palate, which is very well shown; (iii) the vestigial tooth on the right side which is shown in its socket, having apparently never cut the gum, though a depressed ring of the surface of the bone round it suggests that it might perhaps have cut later in life. No fellow to this tooth occurs on the left side. C and D, *Dicynodon* sp., R.514, *non loc.*, a small fragment of a skull and lower jaw in occlusion which has been prepared with acid so that it now shows the upper surface of the roof of the mouth, i.e., the floor of the air passages; the stippled area on each side of the vomer is matrix filling the hinder end of these passages. C, is a drawing of the specimen directly from above. D, is drawn obliquely from above; the middle line is just indicated in the anterior part of the premaxilla, and shown posteriorly as the high flange of that bone. The internal nostrils cannot be seen but they are reached by passing above or below the small bar of matrix labelled Int. Nar. Boss, downwardly directed process entered by a foramen from behind, presumably the posterior limit of the beak. Tooth, vestigial tooth. (Key to abbreviations p. 206).

transferred the point of attachment of the anterior pterygoid muscle from the lower border of the angular to its upper border at the surangular. Where, as in *Diictodon*, it bounds a very extensive space, the nature of its shape and relations is such as to make it highly improbable that it enclosed nothing but a tendinous attachment of a muscle. Its structure in *Diictodontoides* is similiar, and the fact that in *Diaelurodon* it is expanded into a considerable spheroidal shell implies, I think, a functional use, the protection of something surrounding the hinder part of the jaw, which must presumably have been of considerable importance, and of a kind whose function would be lost if it were exposed to external pressures.

It is difficult to believe that the lamina has any functional relation to the ear, for the stapes of dicynodonts is a powerful bone firmly held between quadrate and fenestra ovalis, and does not in fact lie in any close association with it. But the lamina does allow the anterior pterygoid muscle a greater range of action, whilst still providing attachment for a muscle sheet connecting the two rami of the jaw together. Broom, at one time at least, thought that it housed a parotic gland for digestive enzymes, but it seems to me immensely elaborate and universal to have that function only. Other people have been singularly reticent in attributing any function to it.

Thus I have seen no explanation of the function of this structure which will explain its universal occurrence in therapsids from beginning to end of the history of the group.

VERTEBRAL COLUMN

The only complete column available to me is that of *Diaelurodon*, but *Diictodontoides*, *Dicynodon cf sollasi*, *D. pygmaeus*, R. 235, and R.311, are all useful for detail. Comparison with descriptions of other forms confirms that the structure shown in these specimens is found in all essentials throughout the whole group of anomodontia.

Atlas

The paired atlantal neural arches are best shown in *D. cf sollasi* (Fig. 5). Each is articulated by a large, close fitting facet with the upper surface of the odontoid, and bears anteriorly a face directed forward, downward, and inward which articulated with the exoccipital component of the condyle. Immediately above its articulation with the odontoid the atlas bears a powerful transverse process which is deep and notched ventrally, is directed laterally and slightly backward, and rises as a powerful column to expand into an extensive upper surface from which a small neural spine arises, far from the middle line. The proatlas is also paired; each element is a thin sheet of bone resting on the upper and anterior surface of the neural arch of the atlas, and on the occiput above the foramen magnum.

The atlas and proatlas of R.311 are essentially similar, though the atlas is proportionately shorter, and its elements relatively heavier, and the proatlas is a massive bone, half as thick as its width.

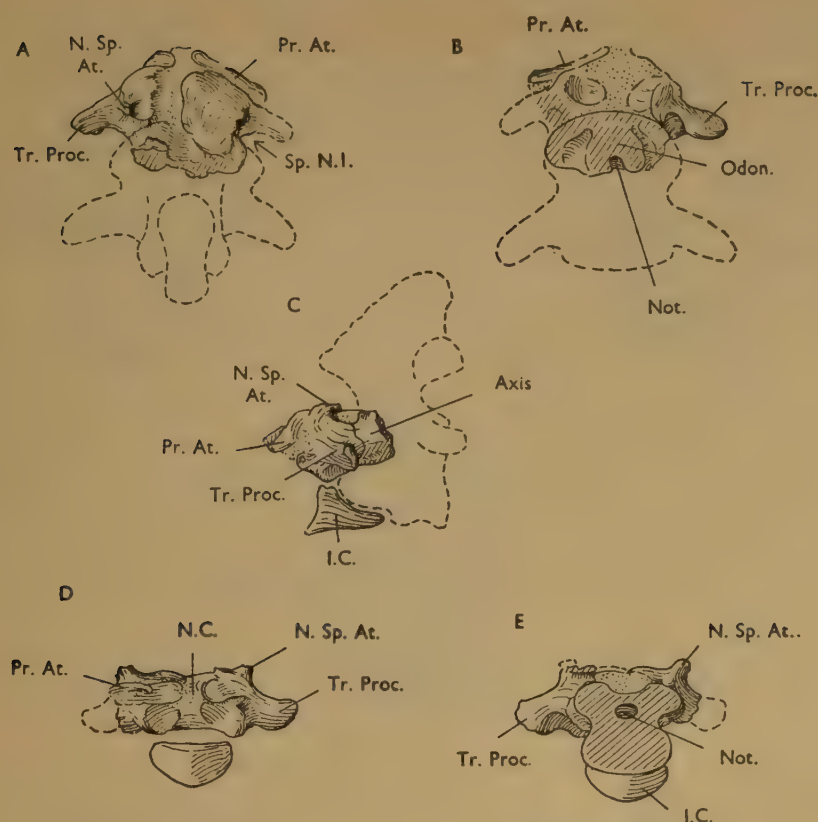


Fig. 5. *Dicynodon cf. sollasi*, ♀, R.53, Upper Endothiodon zone, Kuilspoort Nek, Near Beaufort West, C.P. The atlas, proatlas, and axis of the skull of an individual previously figured (*Proc. zool. Soc. Lond.*, 118; 1948) $\times 4/3$. The drawings represent the specimen as it is preserved, augmented by impressions of the lower part of the odontoid, and the intercentrum, on adjoining pieces of matrix; the outline of the rest of the axis has been dotted in to assist in understanding the structure.

A, from above; B, from below; C, from left; D, from in front; and E, from behind. In B, the odontoid process is broken through horizontally, exposing the notochordal cavity posteriorly, and laterally the grooves which lie below the expanded flanges which support the atlantal neural arches. (Key to abbreviations p. 206.)

Axis

The axis has an odontoid process, usually fused with it, though traces of the suture may persist into large individuals. In R.235 the centrum is rather higher than it is wide, the posterior surface is deeply concave, and the anterior is fused with the atlantal centrum. The odontoid so formed is a remarkable structure; its anterior face bears a small foramen for the notocord, about 1.5 mm. across. The upper surface bears a deep groove in which rested the spinal cord, but it is perforated by a very large hole through which blood vessels passed from the

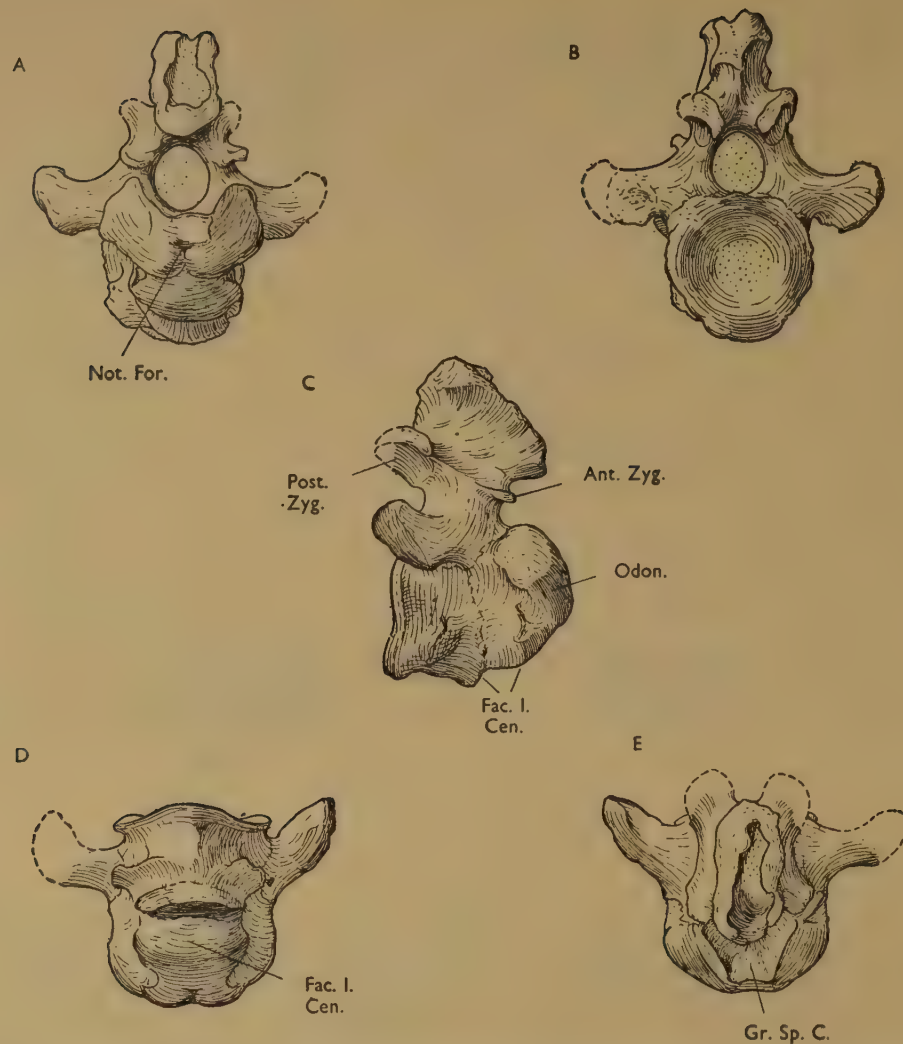


Fig. 6. Isolated dicynodont axis, R.235, from the Cistecephalus zone of the "Schneuberg," $\times \frac{2}{3}$. A, from in front; B, from behind; C, right side; D, from below; E, from above. In E, the foramina for blood vessels in the floor of the neural canal are concealed by the neural spine. (Key to abbreviations p. 206.)

membranes surrounding the cord into the vertebra; an exactly similar hole enters the axis centrum. The rest of its structure may be seen from Fig. 6.

Neck

The trefoil-shaped condyle of *Dicynodon* is characteristic, but is not universally found within the anomodonts; for example in *Tropidostoma microtrema*, and, imperfectly shown, in *D. halli*—which are skulls some 20 cm. long—the condyle is a cylindrical process of small diameter, squarely truncated behind, and showing nothing of its tripartite nature. Such a condyle would probably have seriously restricted movement of the head on the neck, for only articulation of the atlas

on the axis would have allowed any free movement. In normal dicynodonts—where the exoccipital components of the condyle have “spherical” surfaces which fit accurately onto the appropriate facets of the neural arches of the atlas, whilst the basioccipital articulates equally accurately with the intercentrum—free movements, including some rotation under adequate control, must have been possible.

The presence in the axis of definite “anterior zygapophyses” evidently in series with the posterior zygapophyses, (shown well developed in R.235, and in *Diaelurodon*, and less markedly in *Diictodontoides*) suggest that rotational movements of the atlas on the axis, though possible, must have been restricted, as indeed they necessarily were if the spinal cord were of a transverse sectional area at all commensurate to its canal.

In *Diictodontoides* seven vertebrae were disarticulated from the skull and the rest of the body and may reasonably be assumed to constitute the neck (Fig. 7B). In *D. pygmaeus* (Fig. 9) the atlantal intercentrum is followed by five centra before the apparently undisturbed shoulder girdle hides those which follow. *Diaelurodon* shows about five vertebrae between skull and shoulder girdle. Von Huene (1931) gives *D. kolbei*? eight cervicals, and Cox (1959) shows a neck of six vertebrae in *Kingoria*. Thus there is no doubt that dicynodonts had a neck, though its size is difficult to establish without a good set of complete uncrushed ribs, but there is no abrupt change between neck and trunk as in mammals.

The wide separation of the zygapophysial articulations of the cervicals, shown well in *Diictodontoides*, suggests much flexibility in the neck, and the wide intercentral spaces here lend further support to this view. The articulation of the axis with the third vertebra is of some interest, for again the posterior zygapophyses of the axis are widely separated and have large powerful articulations with the prezygapophyses of number three. These lie at less than 45 degrees with the horizontal and again suggest considerable flexibility.

Thus, the head was moveable on a flexible neck, it could evidently reach the ground, or be turned so as to stretch up for some distance. There was probably considerable lateral flexibility anteriorly, becoming less as the thorax is approached. The short overlapping cervical ribs seem consistent with such movements.

Trunk

The rest of the presacral column is best shown in *Diaelurodon* and here consists of twenty-four vertebrae. It is evident that there is a tendency for the vertebrae in the middle of the back to have slightly longer centra than those before and behind them, but in *Diictodon* there are individual variations in central length throughout the column, showing no regular arrangement. There is no distinction between thorax and abdomen, the vertebrae and ribs pass back to the sacrum with no abrupt change of character.

Diaelurodon shows details of many vertebrae in its complete column. By the eighth vertebra the width across the zygapophyses has become much smaller,



Fig. 7. Selected vertebrae from four anomodont skeletons, numbered according to their place in the column. A, R.497, a large dicynodont from the top of the Endothiodon, or bottom of the Lower Cistecephalus zone of the Nieuveltdt, $\times \frac{1}{3}$. It is not possible to be certain of the position in the column of the 21 vertebrae comprising this specimen, but three of them in association seem to be immediately presacral, and the others form a continuous series further forward; vertebra "16" shows the well marked rib articulation lying at the root of the transverse process. B, the type specimen of *Diictodontoides skaioi*, gen. et sp. nov., R.396. Cistecephalus zone, Murraysburg, C.P. $\times 1$. Pit, the "pit" in the lateral surface of the centrum, of unknown function; C, *Diictodon sesoma*, sp. nov., R.314,? Cistecephalus zone, Buffels River, O.F.S. $\times 2$. D, *Diaelurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P., $\times 1\frac{1}{3}$. The transverse process is a small protuberance, and there is a long rib articulation extending from the front border of the centrum towards, but not reaching it.

Vertebrae where necessary have been restored from their neighbours. (Key to abbreviations p. 206.)

and their articular faces, of considerable size, stand nearly vertically, interlock extensively, and suggest considerable power of vertical, but little of lateral movement. By the eleventh and twelfth vertebrae the zygapophysial articular surfaces are again widely separated from the mid-line, and are nearly vertical; they are of good size. By the fifteenth vertebra the width across the posterior zygapophyses has become smaller, but the extent of their overlap seems to increase, and the articular facet of the prezygapophysis is much wider than that of the postzygapophysis that rests in it, its articular surface and that of its fellow being essentially concentric when seen in transverse section. Thus provision is made for considerable dorso-ventral, as well as lateral flexibility. From here backwards the width across the zygapophyses seems to increase until the sacrum is reached, the twenty-eighth vertebra having large, very widely separated pre- and postzygapophyses, the twenty-ninth receiving the postzygapophyses in narrow sockets, evidently little flexible.

Judging solely from the character of the zygapophyses it would seem that the neck was considerably flexible, but the anterior part of the thorax relatively stiff, and presumably connected by cartilaginous sternal ribs to the rib attachments of the sternum. The implication is that breathing movements of a mammalian pattern did occur. Posteriorly the rib movement apparently became less in extent, and may indeed have almost vanished as the sacrum is approached. The complete absence of a definite lumbar region contrasts sharply with the condition in mammals.

The articulated vertebral column above described appears to have been reasonably flexible, less so probably than in small mammals of similar size, more, perhaps, than in many lizards. But any such statement is inevitably subjective.

Evidence from a large specimen

The large column R.497 (Fig. 7A), is useful in making a study of the possible movements of the back, and evidence drawn from it may be used in considering the smaller columns. It shows exceedingly well the nature of rib articulations, and hence the extent to which the great transverse processes exist as muscle attachments, and not directly to support the ribs. The tuberculum of the rib lies essentially at the root of the process, and not at its tip, the implication being that the intervertebral musculature is powerful, thus preventing collapse in the middle of the back. Vertebra no. "9," just behind the neck, has a centrum short in proportion to its width, with a fused neural arch standing immediately above it; the anterior zygapophyses are not widely separated, but they are wider than the posterior zygapophyses, allowing considerable lateral movement. The transverse process is outwardly and upwardly directed, its summit rounded. Its lower surface faces very largely downward, and forms a large articular surface for a rib, whose head (on the left side) is in position. It seems probable that, as in the case of the eighth rib, which lies before it more completely exposed, the articulation is single but widely extended. The rib in a distance of about 3 cm. contracts from a width of 4.5 cm. to one of some 1.8 cm., which it retains for some distance. Succeeding vertebrae show a rise in position of origin of the trans-

verse process. In no. "16," for example, the transverse process is considerably upwardly directed, and is slender, the rib articulation being restricted to its root and lying on a special "pad" two or three millimetres thick, thus the distal part of the process survives only as a muscle insertion. This condition continues back to the sacrum, the last presacral rib having a very massive root.

Thus, the back of *Dicynodon* is powerfully articulated but none the less has a possibility of considerable movement, perhaps particularly dorso-ventrally, though lateral movements were, of course, possible.

Sacrum

The sacral vertebrae and their ribs will be dealt with in connection with the pelvis. *Diictodon* and *Diictodontoides* have three sacrals, *D. halli* and *Endothiodon* four, *U. gracilis* a probable five, *D. kolbei*? five, *Kannemeyeria* and *Lystrosaurus* six. Apparently the number of sacrals becomes greater to serve obvious mechanical needs in larger and later anomodonts. The short neural spines of the sacrum form a transition between the upright spines of the last dorsals and the backwardly sloping spines of the caudals.

Tail

No complete tail of *Dicynodon* is known. Broom says it consists of from eight to twelve vertebrae. *Diictodon*, the only specimen of mine showing it, retains five caudals, diminishing in size so slowly as to suggest that it may have been considerably longer (Fig. 15B). Each has a pair of ribs, short structures fused to the middle of the upper edge of the centrum by a widened head to form a short process. The first two incline forward. The tail as preserved extends to the level of the hinder border of the ischia, where it is broken across, and shows in section a substantial structure, the depth from the top of the neural canal to the mid-ventral ridge of the centrum being quite considerable, and the width from rib tip to rib tip being twice as great. In other words the tail here, if allowance be made for the neural spines and haemal arches, may well have been of nearly circular section, about 15 mm. in diameter. The last preserved caudal vertebra is evidently twisted in position, suggesting a relatively small, mobile tail rather resembling that of a mammal than of a reptile.

Diaelurodon retains two caudal vertebrae, a little displaced, and *Diictodontoides* shows fragmentary remains of two.

Pits in Centra

The vertebrae of *Diictodontoides* have a peculiarity seen developed to a variable extent throughout the vertebral column. This is the presence of a small, deep, and unexplained depression on the centrum, shown especially vividly in the neck. Seen most typically in cervical vertebrae three and four, for example, it lies on the lateral surface a little forward of the mid point of the centrum, and has the form of a relatively deep pit, completely floored by continuous bone, facing directly outwards, with walls which flare outwards when they reach the surface.

The beginning of the story is seen on the atlas, where on the lateral surface of the odontoid there is a matrix-filled opening evidently in series with the one on the axis. The latter is an elaborate structure with a foramen opening forward into a groove which forms, as it were, a spout leading out onto the lateral surface of the centrum, and indeed extends forward by a depression to its contact with the odontoid. Behind this groove a single foramen of comparatively large size opens out independently onto the lateral surface of the centrum. The pit on the third vertebra is about three millimetres wide, a millimetre and a half high, and about a millimetre deep. Its floor is rounded and apparently not perforated by any foramen.

I have not yet succeeded in finding any satisfactory explanation of the function of this remarkable pit. It evidently is not universal in dicynodonts. It is not shown in B.M.N.H. R.3747, in which what is probably cervical five has a perfectly preserved surface lacking any trace of such a structure, or in any of my other material. Its function is not clear: of all possibilities the suggestion that it housed some modified blood vessels seems the most probable.

It may, however, be noted that in a skeleton of a large individual of *Echidna* in the museum of the Department of Zoology at University College, all the dorsal vertebrae possess excavations of the lower surface of the centra, below the position of the rib facet, which present some similarity. They are quite extensive, sometimes freely open downwards, and are very commonly covered imperfectly by a very thin shell of bone continuous with, and indistinguishable from, that which covers the whole of the rest of the surface of the vertebra. Anteriorly in a large skeleton they die out on the last cervical vertebra, and posteriorly disappear on the first lumbar vertebra. *Platypus*, in the two available specimens, shows what is evidently the same condition in a reduced form; irregularly placed, and commonly small, foramina opening into a cavity in the centrum from the ventral surface, sometimes only on one side, sometimes paired. But the condition is much less obvious than in *Echidna*. The nature of these pits seems to be unknown. I have searched all the literature, finding no reference to them.

Ribs

My material shows a continuous series of cervical ribs; the atlantal one I have never seen, but the articulation for it suggests that it was single-headed and was presumably a straight bone. The axis bore a two-headed rib articulating with the downwardly and backwardly facing facet on the transverse process, and with the ventral part of the lateral surface of the centrum. This rib, in *Diaelurodon* Y-shaped, is about the length of two centra, and tapers to a narrow end. Other cervical ribs in my series of specimens are similar, and remain effectively straight, though posteriorly they increase to the length of four centra, forming a transition to the trunk. None the less the eighth vertebra of *Diaelurodon* still has widely separated facets for the capitulum and tuberculum of its rib (Fig. 8), but it appears to be the last with this arrangement, subsequent vertebrae bearing ribs with a single articulation, expanded, but not to the width found in cervicals. The number of cervicals is thus very near that of mammals.

The single-headed ribs of the thoracic region articulate with a facet on the arch and centrum, below the transverse process, whose end they do not touch. The rib articulation back to the twenty-fourth vertebra is powerful. The twenty-seventh vertebra has a small transverse process connected by a slender ridge with the anterior end of the centrum, but the facet for the rib head occupies only a small part of the ridge, extending to neither end. The rib head of the twenty-eighth vertebra is deepened, and the rib not unusually slender. The column bears rib attachments on all the vertebrae and thus shows no indication of any specialisation into thoracic and lumbar vertebrae analogous to that of mammals.

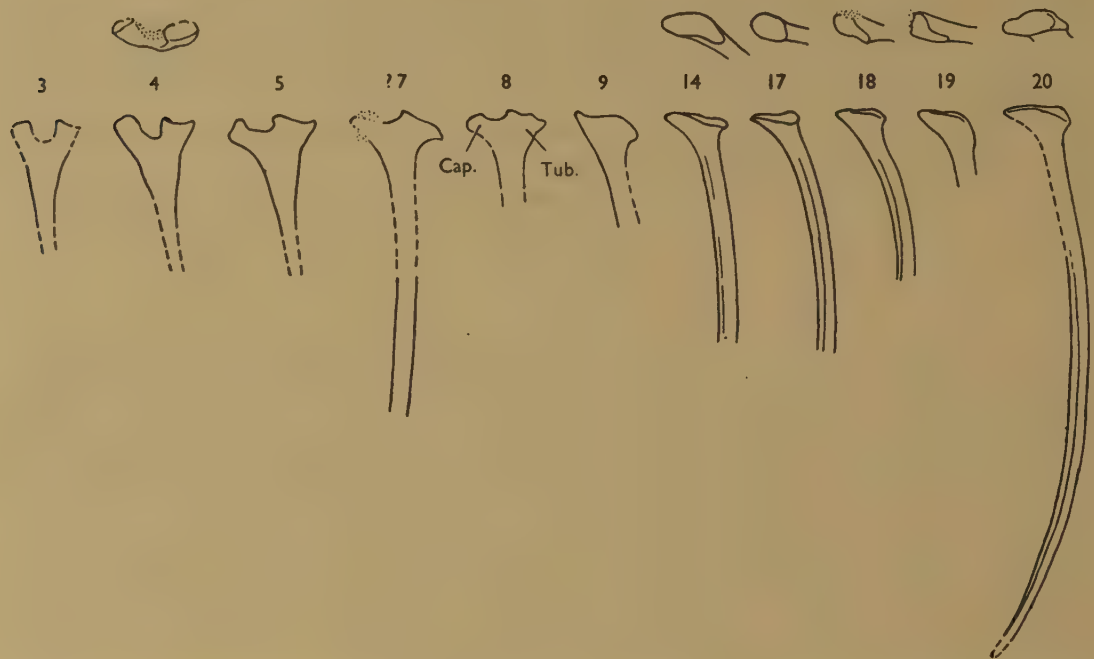


Fig. 8. *Dicaelurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P. x $1\frac{1}{2}$.

A series of left ribs belonging to the vertebrae whose numbers are written above them; the top row represents their articular ends. This is the only series amongst my material which is capable of being drawn; the other specimens, less well exposed, conform to it in essentials. None of these ribs is complete, though no. 20, is very nearly so, and cervical ribs 3, 4, and 5, are evidently nearly complete. The sharp distinction in the mode of articulation of ribs 8, and 9, is very clearly shown. (Key to abbreviations p. 206.)

The ribs are grooved along their length on anterior and posterior surfaces, and are rounded on inner and outer sides. Their curvature is usually that of a very large circle, suggesting a rapidly enlarging body, remaining capacious up toward the pelvis. Posteriorly, however, the body was laterally compressed but deep, the ilium standing up nearly vertically, and the body cavity, left largely unsupported between the outturned pubes, was in fact partly floored by the inturned ischia, which none the less did not meet (Pearson, 1924, p. 842).

Broom's original figure of the skeleton of "*U. gracilis*" (1901), and Seeley's

figure of *Dicranozygoma* (1900), give illustrations of a nearly complete series of ribs, which can be supplemented by those figured and described by Cox (1959). They show that there is no reason, such as exists in cynodonts, to suggest the presence of a diaphragm, the abdominal cavity remaining undivided. None the less breathing movements would have been possible; the long, oblique, rib attachment of the anterior post-cervical vertebrae would ensure that they took place during any co-ordinated rib movements.

Sternum

The sternum is represented by the very small example belonging to the skeleton of *Diaelurodon*, rather concealed by other bones, but showing the general structure well (Fig. 12B.)

Much better preserved is an isolated sternal bone (R.301) from the *Cistecephalus* zone (Fig. 11D & E), which agrees well with that figured by Owen (1880) as belonging to *Platypodosaurus*. The ventral surface of the bone is shallowly concave laterally, and the visceral surface is scooped out on each side to form a very marked depression, facing forward and outward, which must, I think, be related to some structure. It is possible that a cartilaginous extension to the coracoid rested in the depression, which ends posteriorly at a very well marked attachment for the first sternal rib. This attachment passes upward and inward, is of reasonably constant width for its greater part, but widens a little as it passes down to the cartilaginous border of the sternum which continues as cartilage apparently all round it. The second sternal rib is attached to a facet lying behind the first by about its own width, and the third is as much again more posterior. But the distance between the rib facets of the opposite sides decreases very markedly from the first to the third. None of these rib facets shows anything suggesting that it was attached to more than one rib, and the space between them shows an extremely spongy bone surface, full of foramina, sharply marked off from the continuous bone covering the dorsal and ventral surfaces. Finally the sternum ends posteriorly in a cartilage covered surface which is the thickest point of the whole bone, with a keel ventrally, a flat visceral surface, and the last rib attachments quite widely separated at the base of an obvious cartilaginous continuation. The most interesting point about the structure of the sternum of R.301 is that its thickest point is in the mid-line at its hinder end. It seems quite impossible that this can have received the ventral ends of further ribs directly, the implication being that there was a cartilaginous continuation into which such ribs passed. The alternative of an ossified mammal-like sternum seems improbable.

SHOULDER GIRDLE AND FORE LIMB

The position of the shoulder girdle in the body is difficult to determine with any assurance. That it lies behind a neck (as I have shown above, p. 151) is confirmed by several specimens, including a very small *Dicynodon*, a juvenile, R.443,

identified as *D. pygmaeus* by comparison with Broom & Haughton's figure (1917, p. 123). Here the right side of the shoulder girdle is preserved in very nearly natural position (Fig. 9). The anterior border of the clavicle at its junction with

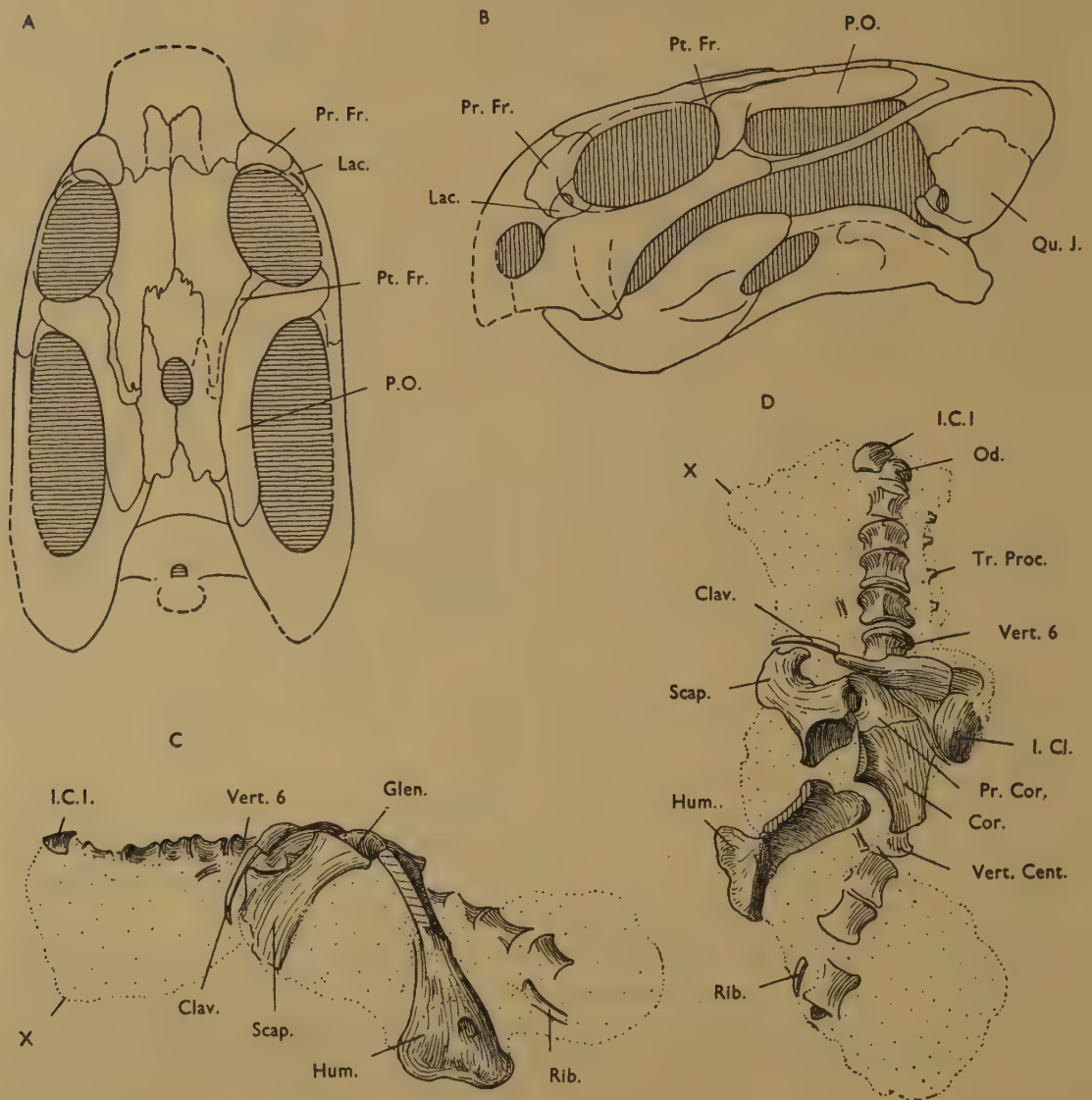


Fig. 9. *Dicynodon pygmaeus* Br. and Haughton, R.443, from the Lower Endothiodon zone, Hans Rivier Dam, Beaufort West, C.P. $\times 1\frac{1}{2}$.

Skull and anterior part of the vertebral column in articulation; this specimen, obviously undisturbed, is the best evidence for the existence of a neck. The widely opened sutures and the unerupted tooth show that it is juvenile. A and B, the skull slightly restored; B, left lateral surface; the full extent of the unerupted canine tooth is shown, as the bone covering it was removed by weathering; C, and D, the neck and shoulder girdle in the matrix; C, right side; D, from below; the point marked X, in the matrix meets the posterior edge of the right squamosal just above the quadrate. (Key to abbreviations p. 206).

the interclavicle lies at the hinder end of the centrum of the sixth vertebra. The coracoidal part of the girdle lies parallel to the vertebral column, with which it is in contact, the scapula (incomplete) inclines much forward as it rises round the chest, and the hinder part of the interclavicle is sphaeroidal in the mid-ventral region, implying a rather narrow chest and a neck which, judging from the nature of the occipital surface of the skull, expanded where they joined.

But it is not easy to reconcile the position of the shoulder girdle *in situ* with its relation to thoracic ribs. The living animals which have some structural resemblance to dicynodonts are the monotremes. In them it is remarkable that the scapulae—large, powerful bones in some ways very closely recalling dicynodonts in general structure—lie so far forward that the first dorsal rib (the first, that is, whose rib articulation joins the anterior part of the presternum) lies entirely behind the shoulder girdle, whose general trend is parallel to it in both *Platypus* and *Echidna*. In both this arrangement seems to be associated with the short neck, widely expanded body, and laterally directed humerus. How far the monotremes are a satisfactory guide to anomodont structure is evidently doubtful. The reduced cervical ribs, for example, are a point of noticeable distinction. Furthermore the presence of an enlarged anterior sternal bone, with which the hinder ends of the interclavicle, and of the coracoid articulate, is a feature probably not paralleled in dicynodonts (cf. Fig. 10). Nevertheless, I have felt it possible to place the scapula rather far forward in the restoration of my three specimens (Fig. 23), despite the fact that it overlaps relatively short cervical ribs, and does not in any way embrace the thoracic region.

Clavicle and interclavicle

The relation of the clavicle and interclavicle to the rest of the shoulder girdle is illustrated in Figs. 9, 10, 11 and 12. The interclavicle obviously varies in shape: in *D. pygmaeus* it is a triangular bone with a swollen mid-ventral shell. In *Diictodon* it is a flat sheet of bone with straight lateral margins passing inwards to a truncated hinder extremity. In *Tropidostoma microtrema* it is T-shaped with a broad posterior shaft and a small triangular process in front. It is difficult to relate these variations with anything functional.

A specimen of *Tropidostoma microtrema** (B.M.N.H. P.6922) shows very clearly

*In the British Museum (Natural History) there is a collection of dicynodont material presented by Thomas Bain which has always been kept together. All of it has the same physical character, the matrix is a hard grey rock weathered to a much lighter colour, the bone is yellow, superficially very much cracked and weathered. The material consists of imperfect skulls and postcranial fragments which may be said to be in identical condition. Seeley (1889, Pls 11 and 12) described an occiput (B.M.N.H. R.868) as the type of *Dicynodon microtrema*, and the posterior part of another skull with a neck in articulation (B.M.N.H. R.866) as the type of *Tropidostoma dunni*. It is evident on consideration of the whole material that the great bulk of it belongs to only one species, as Lydekker recognised in 1890; three out of thirty snouts appear to be different. Presumably *D. microtrema*, having page, or at any rate plate priority, is the accepted name, but in view of traces of palatal teeth on some of the other specimens there is a justification for resuscitating Seeley's generic name of *Tropidostoma*. Thus the correct specific name of these specimens is *Tropidostoma microtrema*. The partial shoulder girdles B.M.N.H. P.6922, and P.6923, belong to this material; and B.M.N.H. P.6924, a right pelvis including ilium, pubis and ischium; and there are also

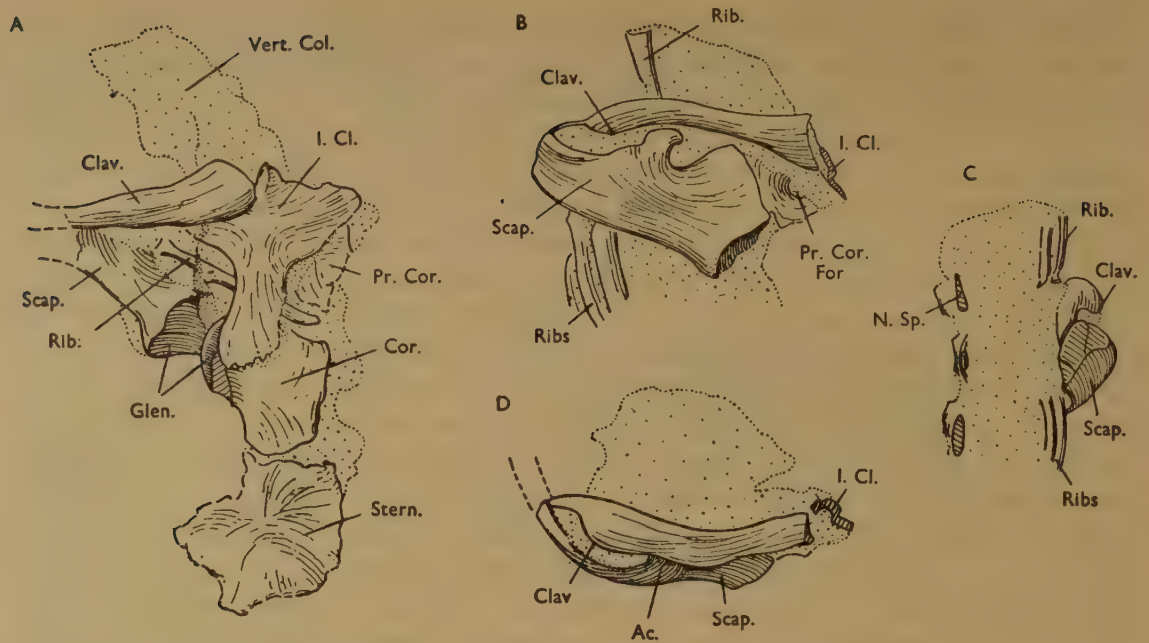


Fig. 10. *Tropidostoma microtrema*, * $\times \frac{1}{2}$ approx. A, B.M.N.H. P.6922 fragment showing the shoulder girdle in natural relation to a section of vertebral column, drawn as preserved; the surface shown has weathered out and received no preparation; B, C and D, B.M.N.H. P.6923, a similar piece of skeleton, showing the mode of articulation of the scapula to the clavicle; B, ventro-lateral view; C, from above, showing the clavicle in natural articulation with the scapula; D, from in front, showing how the clavicle extends above its attachment to the acromium to touch the inner surface of the scapula; in B, C and D, the reference lines Clav. touch the same spot. (Key to abbreviations p. 206).

*see footnote on pp. 159-160.

a good interclavicle, and a clavicle, evidently in natural articulation with it (Fig. 10A). Here the inner end of the clavicle is in contact with the median crest of the anterior end of the interclavicle and passes out almost directly laterally, its slender shaft evidently deeper than it is wide where it is broken off, shortly before it would have met the acromium of the scapula. Another specimen of *T. microtrema* (B.M.N.H. P.6923) from the same material shows the actual tip of the clavicle in articulation with the scapula (Fig. 10 B, C & D). The arrangement is remarkable in that the distal part of the clavicle, like that of *D. halli* (Fig. 11B), is concave and, passing over the acromium process of the

about thirty snouts P.6925-P.6954 some of which show traces of small palatal teeth, while others lack them. Measurements of size on these are almost impossible to make but I found eleven specimens P.6925-P.6935 in which a direct measurement by calipers could be taken—from the mid-line of the snout to the front point of an orbital margin. The measurements cover a range of from 4.7 cm. to 9.3 cm. leaving no interval of more than a few millimetres. There are also about ten occiputs, some fifteen postcranial fragments, and various smaller pieces.

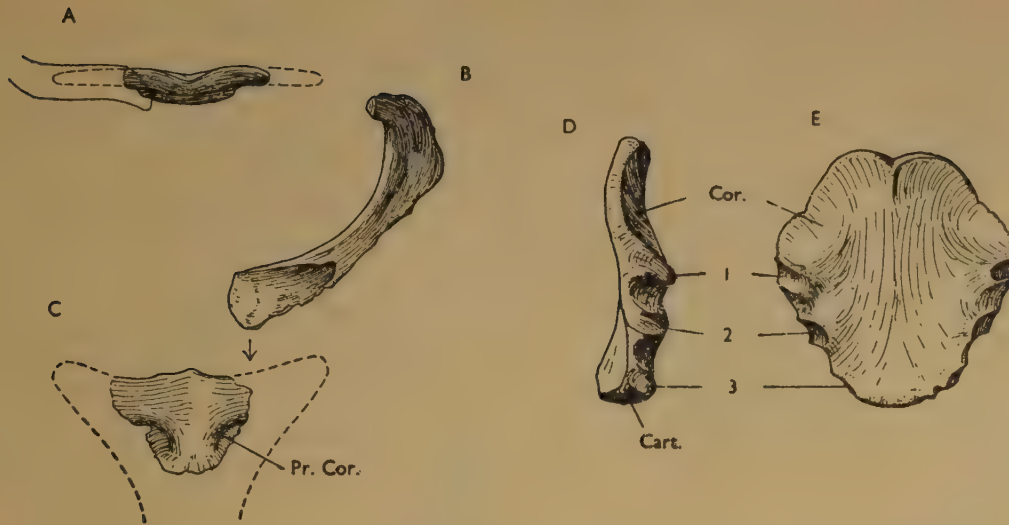


Fig. 11. A, B and C, *Dicynodon halli*, type specimen, B.M.N.H. R.4067, Upper Endothiodon zone (or Lower Cistecephalus zone), Kuilspoor, Beaufort West, C.P. $\times \frac{1}{2}$ approx.

A, interclavicle from in front ; B, right clavicle, visceral surface ; C, interclavicle, visceral surface ; the arrow indicates that the clavicle falls into place on the ventral side of the outer corner of the interclavicle.

D and E, isolated dicynodont sternum, R.301, Cistecephalus zone of the "Schneuberg," $\times \frac{1}{2}$ approx., showing the three sternal rib attachments and the recessed areas in front of them associated with the coracoids ; the thick posterior end is seen below facet 3 ; D, viewed from the left side ; E, the visceral surface.

Cart., facet for a cartilaginous cap, perhaps receiving further sternal ribs ; Cor., depression for a cartilaginous extension of the coracoid ; Pr.Cor., notch for the reception of the anterior and inner corner of the precoracoid ; 1, 2, 3, facets for the attachment of the sternal ribs.

scapula, sweeps round to overlap and to be attached to the inner surface of the scapula far above the level of the acromium. It is reasonable to suppose that this also occurred in *D. halli*.

Cleithrum

One primitive feature of the shoulder girdle which deserves mention is the presence of a cleithrum. Two specimens of mine show this bone. In *Diictodontoides* it is firmly attached to the front edge of what is in effect the acromial crest of the scapula (Fig. 12F), extending out freely beyond the long scapula in such a way as to show that that bone still retained a cartilaginous completion. In *Diictodon* it is similar, but turned down over the cartilaginous cap of the scapula rather more completely (Fig. 12D). This is, perhaps, the last appearance of a cleithrum in the history of reptiles. None of my other specimens show any trace of such a bone.

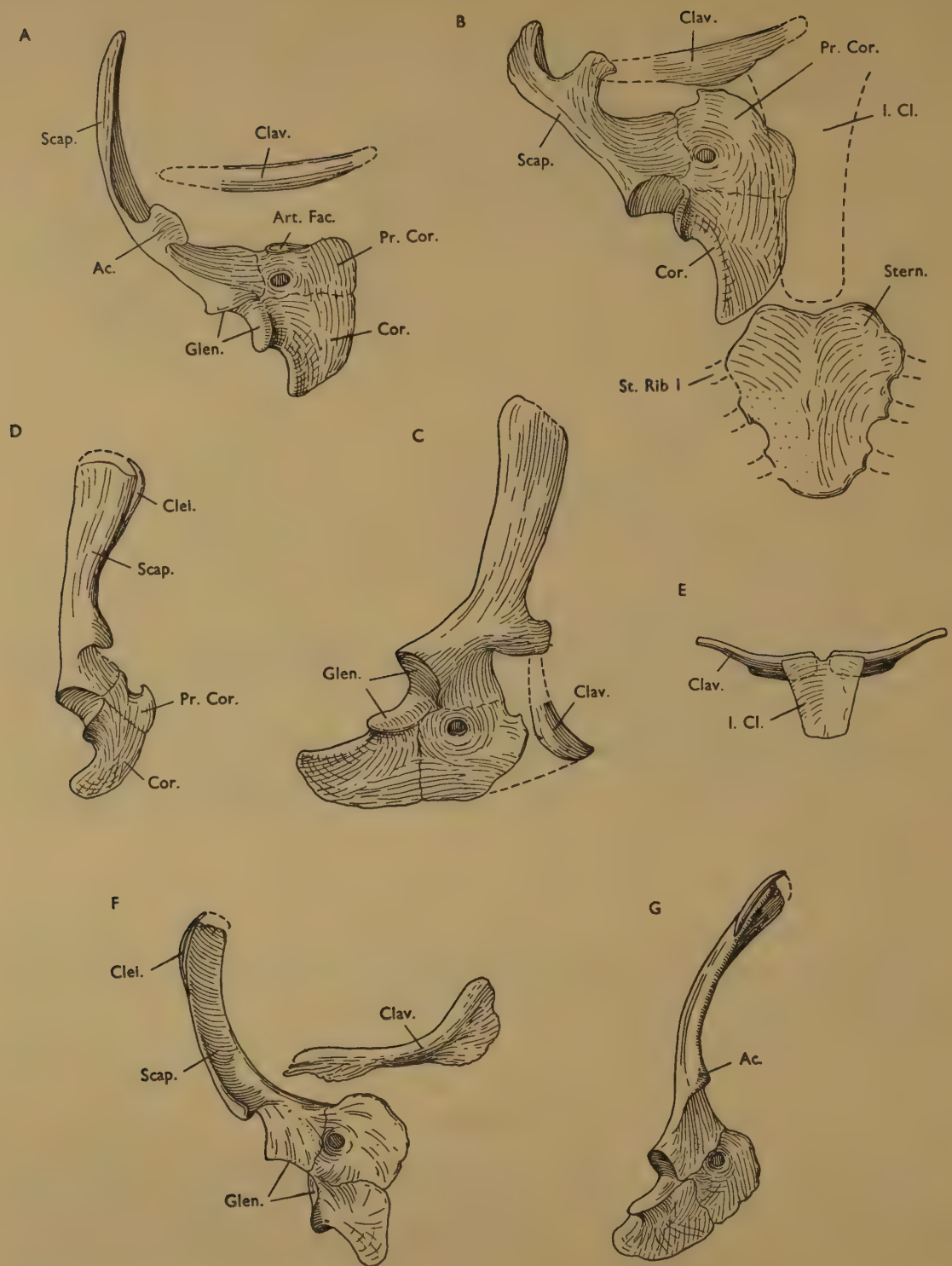


Fig. 12. Anomodont shoulder girdles.

A, B, C, *Diaelurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P., $\times 1\frac{1}{2}$.

D, E, *Diictodon sesoma*, sp. nov., R.314, ? Cistecephalus zone, Buffels River, O.F.S., $\times 1$.

F, G, *Diictodontoides skaios*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg,

[Continued facing page

Scapulo-coracoid, and movements at shoulder

The rest of the shoulder girdle is represented by the splendid type specimen of *D. halli* (Watson, 1917, figs. 12-16), by my smaller animals, equally well preserved, and by the gigantic scapulo-coracoid, R.498. All agree in general structure, often in detail, though there are also differences, as shown in Fig. 12.

In many ways the girdle of the small endothiodont *Diaelurodon* is more easily comparable than the rest with other types of therapsids. In it the coracoid and precoracoid are relatively large, and the scapula less modified from the normal form than it ultimately becomes. The scapula articulates with the precoracoid extensively and has a small, massive contact with the coracoid, so that the glenoid faces of the scapula and coracoid are directly continuous. Little of the glenoid face lies upon the precoracoid, though this closely approaches it. The glenoid surface of the scapula is flat for its greater part, lying essentially at right angles to the glenoid facet of the coracoid, but towards its contact with the coracoid becomes rounded, so that the humerus may be brought forward, perhaps resting on a very small wedge of the precoracoid. The glenoid surface of the coracoid is narrow and has a characteristic cylindroid shape. The arrangement is similar in the very small *Diictodontoides* and the very large R.498, though in the latter the wedge of precoracoid was cartilage-covered and formed a small but definite part of the glenoid cavity (see Fig. 20).

The implication is that the humerus could be brought forward until it lay at right angles to the animal's principal plane, and then be raised or depressed. But in such a position it articulates by so small an area that it cannot have carried much weight; none the less it serves to increase the stride, apparently to a considerable extent. In normal position the humerus trends as much backwards as outwards, and cannot be greatly depressed, so that the length of stride is largely determined by flexure at the elbow.

In *Diaelurodon* the head of the right humerus is free from matrix, and perfectly preserved, and can be tried in place in the glenoid cavity. It is evident that only the scapular facet carried weight, the coracoidal articulation bearing on the side of the bone, probably almost entirely on the cartilaginous head; it is indeed

C.P., x 1.

A, right scapulo-coracoid and clavicle, not articulated. viewed from in front and below ; B, right shoulder girdle and sternum from below, interclavicle suggested by broken lines ; C, scapulo-coracoid and clavicle from right side ; D, right scapulo-coracoid, with cleithrum turned back over cartilaginous cap of scapula, from the side ; note that the precoracoid does not surround the usual foramen, the blood vessel which this transmits notches its anterior margin ; E, clavicles and interclavicle, visceral surface ; F, scapulo-coracoid and clavicle, with cleithrum at the upper end of the scapula ; the clavicle is removed from its attachment to the acromium in order to show the structure, note the overhung tip of the acromium for it, here, and in the other specimens ; G, right scapulo-coracoid from the side ; compare the glenoid cavity with C. (Key to abbreviations p. 206.)

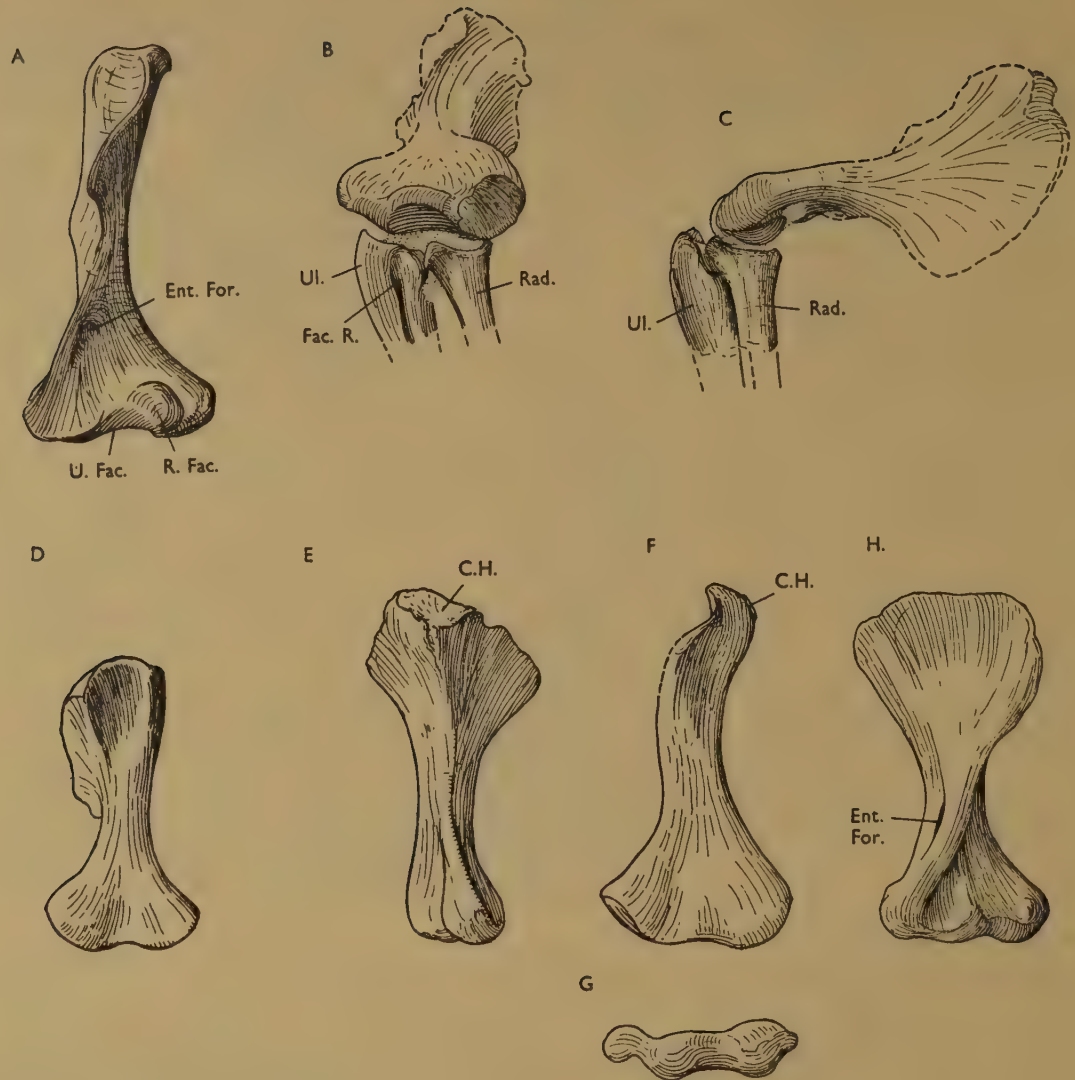


Fig. 13. Anomodont fore limbs to show the variations in shape and proportions.

A, B, C, *Diaelurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P. x $1\frac{1}{2}$.

D, *Diictodon sesoma*, sp. nov., R.314, ? Cistecephalus zone, Buffels River, O.F.S. x 1.

E, F, G and H, *Diictodontoides skaioi*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P. x 1.

A, left humerus from in front ; B and C, the right elbow joint, as it is preserved ; the radius and ulna have slipped a little to the left, and also with respect to one another ; the completely free humerus of *D. halli* was used in restoring the bone ; D, left humerus from its hinder surface ; E, F, and G, right humerus (E and F, are at right angles to one another) ; H, left humerus, G, the distal articular surface. It will be seen that H is difficult to relate to E and F, although they are left and right bones of the same individual ; the differences are due to distortion and depend on the fact that one (H) lies in a matrix compacted without the formation of a nodule, whilst the other (E and F) in a nodule retains its original shape little if at all altered. (Key to abbreviations p. 206.)

evident that the cartilage of the cavity was so extensive that no part of the actual bone preserved on the head of the humerus came into direct contact with the shoulder girdle.

It seems clear on a consideration of *Diictodon*—whose shoulder girdle, perfectly preserved and little distorted by pressure, surrounds the anterior part of the trunk, and whose left foreleg is complete in natural articulation from the humerus to the ends of the digits, and lies actually in position in the glenoid cavity—that the articular surface of the humerus lay about half way across its breadth, and was mainly in contact with the flat glenoid face on the scapula, the more rounded glenoid face on the coracoid coming into contact with the lower surface of the humerus at a point where that bone is thickest, so defining the point of articulation.

Lower limb and movements at elbow

In many dicynodonts ossification of the limb bones is rather scanty, leaving thick articular cartilages, so that it is difficult from the bones to determine possible movements. But *Diaelurodon* is well ossified and does give good evidence. It has a very well preserved elbow joint, which shows the general nature of the articulation and allows some judgment to be made of its flexibility. The proximal ends of the radius and ulna are very nearly in position with respect to the distal end of their humerus, and are perfectly preserved. It is evident that the radius fits accurately a mammal-like groove in the ulna, so that the two bones form a continuous articular surface. The head of the radius is concave for the corresponding facet of the humerus. The ulna clearly extended so that it embraced the end of the humerus, and could slide round it. It is evident from Fig. 13B and C, that the joint can straighten out quite considerably, and it is probable that in full extension of the forearm the radius and ulna can be brought, not entirely into the axis of the humerus, but perhaps to some 135 degrees to that trend, and furthermore it is possible that a little further flexure is allowable.

If this be true then the body could be raised considerably above the ground, with the tracks of the fore feet of opposing sides considerably separated, and the stride was probably longer than at first appears probable, especially when the character of the glenoid cavity and the nature of the head of the humerus are taken into account.

This apparent freedom of movement cannot necessarily be found in all anomodonts.

In the case of *D. halli*, trial with the actual bones is possible. This suggests that the humerus may be brought down, not entirely vertical, but nearly so, and raised into the position in which it is illustrated in Fig. 16 (*Watson, 1917*), except that in this drawing the head of the humerus should be separated from the scapula by two or three millimetres of cartilage. But this is an extreme position, nearly that of rest. Trial at the elbow suggests that when it is extended as far as possible the forearm may be at about 135 degrees with the humerus, and hence the humerus stands more vertically, so that the body is raised considerably above the ground and the stride is longer than I had earlier believed.

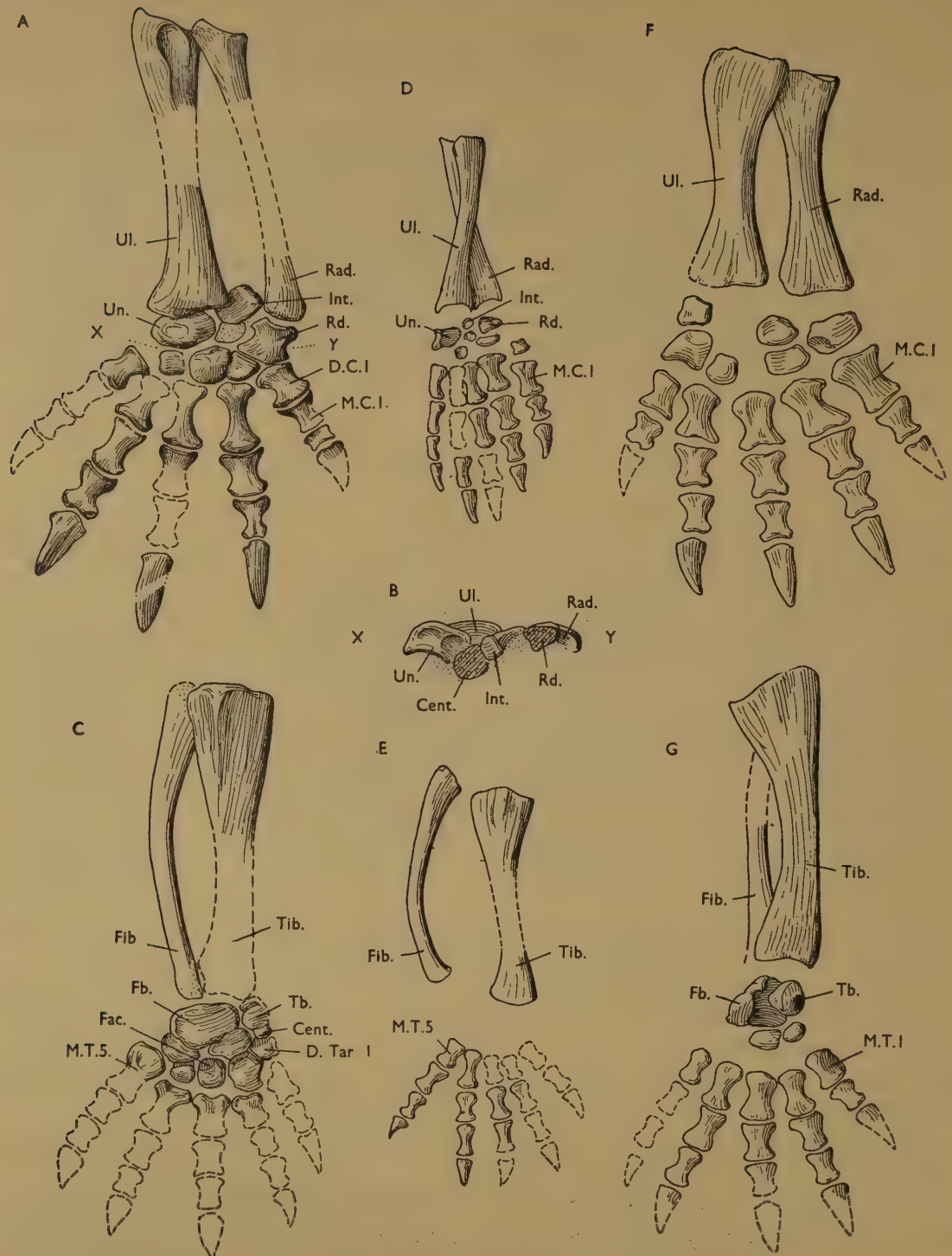


Fig. 14. Hands and feet of anomodonts.

A, B, C, *Dialeurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P., x $1\frac{1}{2}$.

D, E, *Diictodon sesoma*, sp. nov., R.314, ? Cistecephalus zone, Buffels River, O.F.S., x 1.

F, G, *Diictodontoides skaioi*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P., x 1.

A, right lower arm and hand, upper surface, drawn as displayed in the matrix, except that

[Continued facing page]

At the same time the track is narrowed from the pelycosaur condition. General considerations, including the evidence of footprint slabs of Upper Permian age from Cummingstone and elsewhere, show that the stride and distance apart of the hind feet must agree with that of the fore feet, so that it seems that the femur projected a good deal laterally and that the knee was considerably bent in ordinary locomotion. Thus the track made by *Dicynodon*, though wide, shows a considerable stride, the footprints being well spaced, as in Huxley's slab from Cummingstone, called *Chelichnis megachirus* (1877), or Clayden's (1908) similar form from Exeter.

Such a bone as the humerus shows much greater variation in shape in the group anomodontia than one is inclined to expect from a summary inspection, and it seems clear that these variations are associated with a considerable range of habit amongst the members of the group.

Carpus and hand

Part of the shafts of the radius and ulna of *Diaclurodon* are missing, but their distal ends (in an independent block) are well preserved, though a little worn on the outer surface. The radius and ulna separate as they meet the carpus, and between them lies an intermedium, a small shapely bone which articulates with a proximal carpal on each side (the ulnare and radiale). The ulnare is a large bone, rounded when seen from its dorsal side, with a well rounded surface towards the intermedium; proximally it bears a recessed facet for the ulna. The distal articular surface of the intermedium is flat and directed towards a misplaced carpal, no doubt a centrale, seen only in section where the carpus is broken across (Fig. 14B). The distal row of the carpus includes four bones. The fourth carpal

carpals and phalanges have been aligned (see also Fig. 13B and C). The resemblance of the claw phalanges to those of *Echidna* is striking. A gap is shown in the claw phalange of digit 3, the surfaces facing it do not show the structure to be expected in a broken bone: is it perhaps an old fracture not co-ossified by healing? B, the break across the carpus at X Y, viewed from the distal side; C, left lower leg and foot from the plantar surface, articulating with the femur shown in Fig. 17A, B, C. The tarsals and proximal ends of the metatarsals are drawn as they lie in a small isolated nodule. The facets visible on the proximal surfaces of distal tarsals 2, 3, and 4, show that in life the proximal part of the tarsus articulated with them at an angle, making an effective intertarsal joint; D, left lower arm, carpus and hand, palmar surface, drawn as they lie in the rock; the humerus in Fig. 13D, is in natural, or nearly natural, articulation with them, and with the glenoid cavity in Fig. 12D the bones evidently held in position by their ligaments until completely buried in dust; E, right lower leg and foot, dorsal surface; the foot, very incomplete, is drawn as it lies in the matrix in association with the tibia and fibula, which themselves articulate with the femur shown in Fig. 17D and E; F, left lower arm and hand, palmar surface, slightly restored from the right; it articulates with the humerus shown in Fig. 13E; G, left lower leg, ankle and foot, plantar surface, partly restored from the right foot; the tarsus is drawn as it is shown in the specimen. (Key to abbreviations p. 206.)

is small, rather rounded, and not very well preserved. Mesially there is a considerably larger bone of definite shape articulating with a wedge-shaped element, itself articulated with the radiale. The distal surface of these last two carpals supported a bone which appears at first sight to be a metacarpal, but actually is the first distal carpal. This bone articulates also with the metacarpal of digit 1. All five metacarpals are present, though partly hidden; 1 and 2 are seen complete, 3 is very nearly so, 4 shows only the distal end, and 5 is a little displaced. Fingers 1, 2, 3, and 4 are all shown, including their claw phalanges, so that their nature is evident. The number of phalanges follows that of all mammals.

The well developed proximal facet of the claw phalange seems to articulate closely and accurately with the more cylindrical distal articulation of the second phalange. The individual claw phalange is, at its base, about twice as wide as deep. It is long, narrow, downturned at the tip (which is still wider than deep) and it suggests—especially in comparison with that of a monotreme—that the claws in life were very long, probably as long, or even longer, than the individual finger between the metacarpal and the claw. Claws of this type, which are wider than their depth, are clearly not appropriate to a carnivore: they may reasonably be interpreted as digging structures, the nearest parallel to them being found amongst the living monotremes, in which they are notoriously both long and powerful; both *Platypus* and *Echidna* use them for digging. In the case of *Echidna* this is done with enormous efficiency: I have seen an *Echidna* digging itself straight down into a rotten log of wood until it was flush with the surface within a very few minutes.

The fore foot is considerably bigger than the hind foot, as it would have to be to carry the weight of the head and anterior part of the body, in contrast to the more slender hinder part of the body and negligible tail. The break in the carpus of *Diaelurodon* enables one to see the structure and mutual relations of some of the carpal bones, but the most striking general feature exhibited is the dorso-ventral thinness of the structure, which probably implies a considerable flexibility of the fore limb on the hand.

PELVIS AND HIND LIMB

Dicynodont and pelycosaur pelves compared

Helga Pearson (1924) showed that in a large dicynodon, and in *Kannemeyeria*, there is no ventral contact between the two ossa innominata, although *Lystrosaurus* has this contact. The significance of this deserves further discussion.

In all pelycosaurs—a group which includes therapsid ancestors—the pubes and ischia of opposite sides meet in a powerful ventral symphysis which, in *Dimetrodon* for example, is immensely elongated and thickened. Deinocephalia and dromosaurs retain the symphysis between the pubes and ischia of opposite sides: so do all theriodonts. Orlov, in an English translation (which I have seen in type-script) of his paper of 1958, says of the deinocephalian *Titanophoneus potens* that “the inferior symphysial section (of the ischium) is thin, its margin

evidently did not ossify completely, and was girdled with cartilage. The anterior margin, downwards from the junction with the pubis and acetabulum, is also uneven, and evidently had a cartilaginous extension."

Thus it is anomodonts (apart from *Lystrosaurus*) which are peculiar, and it is interesting to speculate on the significance of the development and retention of this loss of contact in them*. In the small endothiodon *Diaelurodon* as well as in

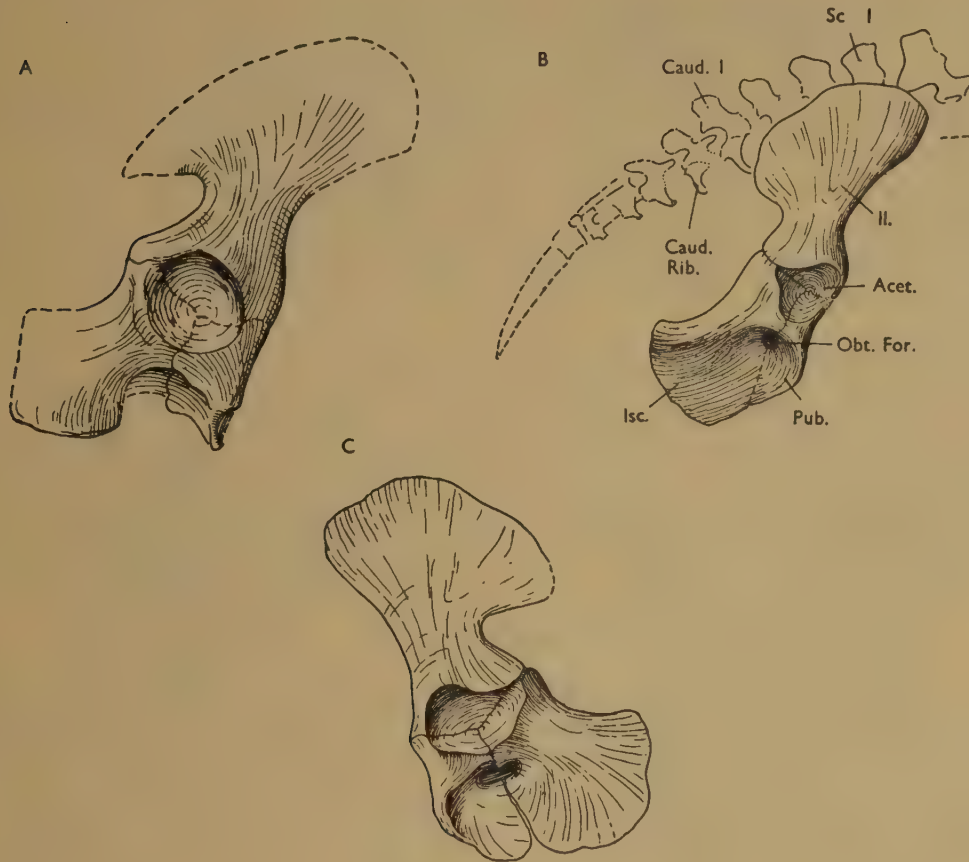


Fig. 15. Anomodont pelvises.

A, *Diaelurodon whaitsi*, Broom, R.451, Lower Endothiodon zone; Beaufort West Commonage, C.P., the right side of the pelvis from without, $\times 1\frac{1}{3}$.

B, *Diictodon sesoma*, sp. nov., R.314, ? Cistecephalus zone, Buffels River, O.F.S., the right side of the pelvis in natural articulation with the vertebral column (from the last presacral to the end of the tail, so far as it is preserved), as it lies in the specimen, $\times 1$.

C, *Diictodontoides skaios*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P., left side of the pelvis from without, $\times 1$. (Key to abbreviations p. 206.)

*The dicynodont condition, which is obviously less good mechanically than the ancestral pelycosaur structure, might be an adaptation enabling the animal to lay a bigger egg. Egg-laying is perfectly compatible with existing conditions, when the Karroo climate was probably similar to that of today—hot in the day and cold at night—for the tortoise regularly lays eggs and buries them in the soil, and it is a "successful" animal.

Dicynodon the articulations between the sacral vertebrae, their ribs, and the ilia are very powerful (although in the latter they are not fused in any specimen known to me), presumably as a compensating device for the loss of the ventral contact.

The pelycosaur pelvis, very well described by Romer & Price (1940), is remarkable because the ventral part extends greatly on each side of the acetabulum, whilst the relatively small ilium, though carrying the whole upper part of the acetabulum, is reduced dorsally to a relatively small sheet of bone attached to two sacral ribs. In early forms the attached part is a narrow posterior projection, whilst in more advanced animals the posterior projection becomes proportionately smaller and an anterior projection comes to play an increasing part in contact with the sacral ribs. The acetabulum faces outward and—there being a trace of a buttress from the ilium above it in some forms—perhaps a very little down. But the anteroposterior length of the ventral surface of the pelvis is always very great, the implication being that the femur was directed laterally, almost parallel to the ground. The lower leg, which could not be closed against the under surface of the thigh owing to the rather inflexible knee joint, is directed downwards and outwards, so that the track made by the hind feet is very wide, as indeed was that of the fore feet.

In dicynodonts the conditions, though variable, never conform to the pelycosaur pattern. It is evident that the pelvises of the four anomodonts which are before me differ very considerably from one another, and clear that the differences cannot be accounted for by the varying size (i.e. weight) of the animals of which they formed part, for three of them (*Diaelurodon*, *Diictodon* and *Diictodontoides*, Fig. 15), are of similar small size, the fourth, *D. halli*, being large.

Dicynodon halli

It seems convenient to begin with a description of *D. halli* (B.M.N.H. R.4067), since the animal is large, and possible articulations can be tried directly between the isolated and well preserved limb bones. The sacrum, with the ilium articulated in natural position on the right side, and much of the pubis and ischium, is well preserved. The centra of the four sacral vertebrae, and the first "caudal," are very closely pressed against one another, and are probably fused. They are immobile, though they retain perfect zygapophyses. The anterior pair of zygapophyses of the first sacral vertebra are relatively widely separated, though less so than those of the lumbar vertebra with which they articulate. The posterior zygapophyses of this vertebra, very narrow across, are short antero-posteriorly, but apparently not fused with their opponents. The zygapophyses of the three following sacral vertebrae are very narrow, fused with one another and with the first postsacral "caudal" vertebra, which seems to be movably articulated to the second caudal. The third caudal has a movable articulation and no later ones survive. The neural spines of sacral and caudal vertebrae (all broken off short in the type specimen) are slender.

Both anterior and posterior ends of all these centra are larger than the middle, and the attachment of the sacral ribs, high at first so as to leave the lower half of the centrum free, rises further as they are traced back until in the fourth sacral

the rib articulation only just impinges on the centrum. The sacral rib is very large and is attached to both centrum and neural arch as a continuous fused mass which widens distally, so that the iliac articulations of the hinder three are continuous, the first being separate, at least on the left side.

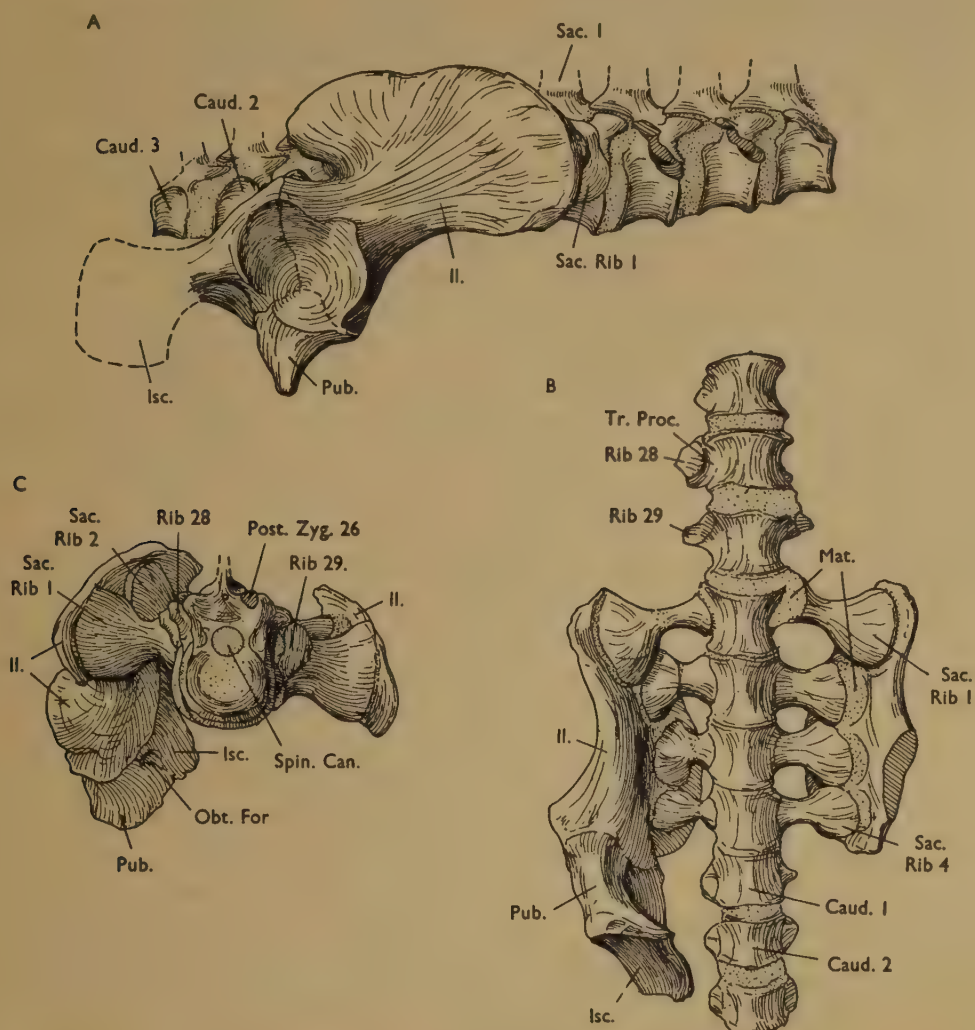


Fig. 16. Sacral region of *Dicynodon halli*, B.M.N.H. R.4067, Upper Endothiodon (or Lower Cistecephalus) zone, Kuilspoort, Beaufort West, C.P., $\times \frac{4}{5}$ ths.

A, from the right ; B, from below ; C, from in front ; the pelvis is very nearly in natural articulation. Mat., dotted areas referred to above. (Key to abbreviations p. 206.)

That the first sacral rib is not fused to the centrum, though its successors are, is vividly shown by the fact that the left ilium has slipped outwards, taking with it the first sacral rib—which is separated from the sacrum by nearly a centimetre of matrix—whilst the three succeeding sacral ribs remain firmly fused to their vertebrae, and are separated from the ilium by a strip of matrix decreasing from about a centimetre to half that thickness.

In the very similar sacro-caudal vertebra the small incomplete rib is probably entirely on the neural arch. It is to be noted that the sacro-caudal vertebra has wider prezygapophyses, although its posterior zygapophyses are still very narrow. The sacro-caudal and two caudal vertebrae preserved shorten very rapidly, but do not become of smaller cross-sectional area. The last preserved does not reach the hinder end of the ischium, of which a good deal is missing.

It is thus evident that the ilia have an extended attachment to a rigid region of the vertebral column, a matter of importance because the centre of the acetabulum lies posterior to any part of the sacrum, and there is no ventral symphysis of the girdle to give mechanical strength.

The completely preserved pubis is short, massive, firmly attached to the ischium by a flat sutural surface, but separated from it by a small obturator foramen, measuring about 1 cm. across, which has much more the appearance of a foramen for a blood vessel than of a large opening through which muscles pass. The pubis meets the ischium and ilium in the usual triradiate suture and forms a relatively small part of the acetabulum, the area of acetabulum on it being less than half of that on the ischium, and a smaller proportion of the iliac surface. It is quite evident that the pubis and ischium did not meet their fellows of the opposite side in symphysis; they may, in fact, have been separated by some 4 cm.

The well preserved pelvis B.M.N.H. P.6924 associated with *Tropidostoma microtrema* agrees very closely with that of *D. halli*.

The femur of *D. halli* is long, well finished, and of characteristic shape; both right and left are preserved and agree closely. The head is directed much more proximally than laterally, and is fitted into a rather shallow acetabulum, implying that the ventral musculature of the pubis and ischium, which is inserted into the lower face of the femur, must have been powerful, carrying in practice a great deal of the animal's weight. The rounded head of the bone, which carried a large cartilaginous cap, is turned a little upward and forward when the shaft lies horizontally. It was continued into a thick, cartilage-covered trochanter, bounded by a powerful trochanteric ridge, which joins the shaft of the bone halfway along its length. This ridge, which evidently bears a muscle insertion extending along it for nearly 5 cm. (in a bone 14 cm. long), is separated by 5.5 cm. from the inturned head of the bone. Seen from the upper surface the shaft passes out from the head in a smooth concave curve to the knee, where the bone is a little over 4 cm. wide and has a maximum thickness of just under 3 cm. The distal end of the bone (only satisfactorily shown in the left femur) makes it clear that there was a thick cartilaginous cap on which the articulations of the bones of the lower leg lay, and that the contact was almost entirely with the head of the tibia, the fibula having a very small footing on it.

When in position in the acetabulum the femur can be taken forward in a horizontal plane to about 45 degrees to the main axis of the body, and go back to 90 degrees, a range of about 45 degrees. The distal end of the femur in a more vertical position (i.e. with the knee nearer the ground), when rotated, can be brought still further back.

It is evident that so much cartilage remained about the knee joint that it is very difficult to judge how much movement was possible there, but I think that

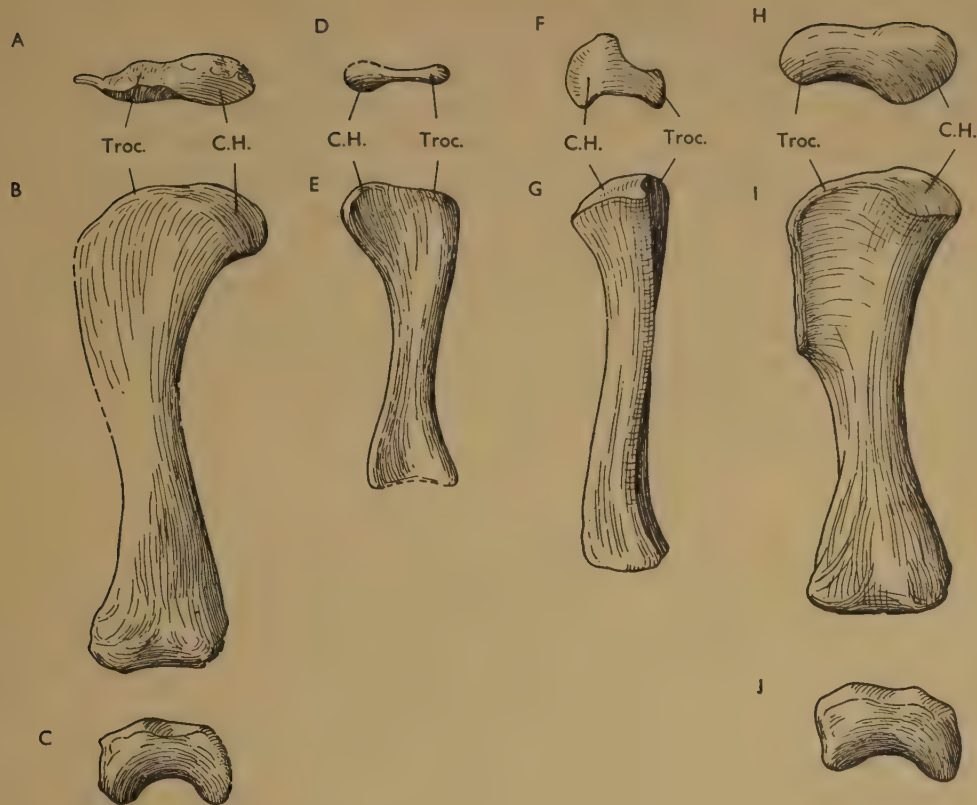


Fig. 17. Anomodont femora of the right side.

A, B, C, *Diaelurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P., $\times 1\frac{1}{3}$.

D, E, *Diictodon sesoma*, sp. nov., R.314, ? Cistecephalus zone, Buffels River, O.F.S. $\times 1$.

F, G, *Diictodontoides skaïos*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P. $\times 1$.

H, I, J, *Dicynodon halli*, B.M.N.H. R.4067, Upper Endothiodon (or Lower Cistecephalus) zone, Kuilspoort, Beaufort West, C.P. $\times \frac{4}{5}$.

A, proximal end viewed along the shaft ; B, from above at right angles to its length ; C, from the distal end ; D, proximal end ; E, from below (this femur is shorter than its fellow, see p. 176) ; F, proximal end ; G, from below (nearly at right angles to the position of F, it is therefore nearly at right angles to the other comparable views) ; H, proximal end ; I, from above ; J, from the distal end. (Key to abbreviations p. 206.)

there can be no doubt that the lower leg could be completely straightened out, and that it could be hinged back so that it was in effective weight-carrying articulation at a little less than 90 degrees with the femur. Indeed, in lateral view the articulation for the tibia faces as much downwards as outwards, forming a face on which it can slide; the shaft of the tibia can be in a vertical position, or even incline slightly inwards. The leg would thus move in a mammal, rather than in a lizard fashion. The condylar surface of the distal end of the femur does not, however, extend relatively so far down onto the lower surface as it does in the very much smaller *Diaelurodon* in which, indeed, all the bones seem to be

much more completely ossified. But in principle there does not seem to be much difference between the two forms.

The lower ends of both right and left tibiae of *D. halli* are nearly circular in section, flattened distally but coated with a cartilaginous cap whose relation to the ankle is not known. The fibula, preserved as an upper and lower end, some of the shaft being missing, can be compared with the fibula of *Diictodon* (Fig. 14E). The proximal end is considerably flattened, obviously having a very small contact—if any—with the head of the tibia, and little with the femur. It apparently separates from the tibia, its shaft becoming slender with a flattened outer and a rounded inner surface, the bone then widening a little to end in a triangular, cartilage-capped face which presumably articulated with the calcaneum.

Not enough materials of the foot remain to make any description or judgment of movements possible.

Diaelurodon whaitsi

The general shape of the side view of the pelvis is shown in Fig. 15A, and agrees very closely with *D. halli*. The sacrum is poorly preserved but the right os innominatum is nearly completely shown. It is somewhat mammal-like, the iliac blade (whose upper border is incomplete) contracting to a relatively narrow neck, below which it expands again to the contacts with the pubis and ischium. The sutures between the ilium, pubis and ischium seem to be completely fused within the acetabulum, but are rather faintly indicated on its borders. The acetabulum, extremely well preserved, is an almost hemispherical pit, rather accurately circular and of considerable depth (3.6 mm. deep and 8.75 mm. across), directed almost at right angles to the median plane of the animal. The ventral parts of the pubis and ischium extend essentially directly downwards, and downwards and backwards respectively. They are separated at the limit of the thickened rim of the acetabulum by a small obturator foramen, below which they seem just to meet before being produced into the short process of the pubis which extends in towards the middle line, and the much longer sheet of ischium, nearly parallel to the animal's length. It is evident that the thin edges of these bones (about 0.5 mm. across), though probably cartilage capped and thus capable of growth, did not in fact extend appreciably further during life.

The femur is remarkable for its mammalian appearance (Fig. 17A, B and C). It has a long and relatively slender shaft, ending in a head which projects inwards in a thoroughly mammalian manner, a trochanteric ridge passing out from it to form, as it were, a capping to the shaft. The head is therefore fitted to articulate with the deep acetabulum so that the bone can be brought straight down to the ground, and can swing with its shaft parallel to the animal's mid plane for the lower half of a circle. This implies that the track may have been unexpectedly narrow: perhaps only some 4 cm. across between the inner borders of the hind feet, when the stride may have been perhaps as much as 10 cm. at the knee. To this has to be added a considerable amount for the movement of the lower leg at the knee joint and ankle, so that the stride, even if only one leg was moved at a time, may well have been some 15 cm., the length of the animal between pectoral

and pelvic girdles being about 22 cm. The distal end of the femur is well finished so that its articular surface can be completely envisaged. The cylindroid articular surface is produced back parallel to the shaft and shows a popliteal fossa, but there is no patellar groove as in a mammal. It is evident that the knee joint can be bent down so that the tibia is at least at a right angle to the femur, though not closed against the lower surface of the thigh.

The right tibia (Fig. 14C), has a well preserved head, but the greater part of the shaft is missing. The articular surface at the knee lies at right angles to the length of the bone, is mainly flat, but shows some trace of two depressions which no doubt in the cartilage cap received the two separated condyles on the lower end of the femur. Below the head the bone is three sided in section, the fibular side bearing a wide shallow groove, a little overhung by an out-turned border of the articular surface. This no doubt housed the upper end of the fibula.

The fibula is preserved complete and shows that the bone is considerably curved, bowing out from the tibia exactly as does that of *Diictodon*, and presumably of *D. halli*. Its proximal end, only partly exposed, is a rounded articular surface for the femur, the distal end, somewhat inturned, widens a little to form a foot, no doubt for articulation with the calcaneum.

The tarsus, shown better in *Diaelurodon* than in the other specimens, is preserved in a small flat nodule, one side of which exhibits the base of four of the metatarsals, together with all the tarsals. The distal end of the fibula is included, but is so featureless that it is not very informative, and the end of the tibia is missing. There are two proximal tarsals, one of which, the calcaneum (fibulare) on the fibular side is very large. It is essentially flattened, and half its proximal face, somewhat damaged, clearly provided a cylindroid head articulating with the fibula, or with a cartilaginous extension of it. The other half shows that it must also have articulated with the tibia.

In the distal row a fifth tarsal fits tightly on the outer peripheral part of the calcaneum, and itself articulates with a fifth metatarsal with an enlarged upper extremity, and with a small fourth distal tarsal, which also articulates with the corresponding fourth metatarsal. The third distal tarsal is similar, but does not reach the calcaneum; its proximal surface is divided into oblique articular facets which receive the hinder ends of the centrale (navicular) and the fifth distal tarsal, implying that the ankle was raised. The large second distal tarsal articulates directly with the navicular and mesially with the first distal tarsal; it is uncertain how far it has a contact with the third distal tarsal. Its metatarsal is also incompletely preserved, but has no special peculiarities. The first digit is completely lost, but a group of tarsal elements, not completely preserved, is present for its accommodation. It seems evident that the foot was widely spreading and very much smaller than the hand.

The hind foot of dicynodonts is always smaller than the fore foot, simply because—owing to the overhang of head and neck anterior to the shoulder girdle—the load carried by the fore limb in animals with a normal stance and a small tail is always greater than that imposed on the pelvis. The marked contrast in size and in spread of the hand and foot in *Diaelurodon*, and even more so in *Diictodontoides*, is thus merely an exaggeration of a condition found usually in anomo-

donts, and indeed in quadrupedal animals, e.g. horses, in general. But it has produced a pattern which does recognisably differ from that of the few other early reptiles whose skeletons are known.

Diaelurodon and *D. halli* are very similar in their limbs, though *Diaelurodon* is a quarter the size, and are presumably capable of similar movements, but in *Diaelurodon* the pose of the hind leg is more advanced in a mammalian direction. This may be partly because it is a smaller animal whose bones are evidently more completely ossified than in *D. halli*.

Diictodon sesoma

The two ilia are nearly in articulation with the sacrum, and the sacral ribs and centra are entirely hidden. The three sacral vertebrae are indeed represented only by their rather tall and narrow neural spines, which are well separated and have thickened and rounded upper ends. The blade of the ilium (fig. 15B) is a thin sheet of bone, incomplete above on the left side, which shows, however, the massive acetabular surface in articulation with the powerful ischium and small pubis. The articular surfaces on the ilium for the pubis and ischium are of unequal length, and the ischium is produced into a wide backwardly directed sheet; the pubis is shorter, downwardly directed, and probably narrower than the ischium. On both sides the acetabulum is largely hidden by the head of the femur, and by intractable matrix, but the rounded head of the left femur is well shown, and implies that it was a deep spherical pit. The ilium carries a projection above the acetabulum which provides the most dorsal part of the facet for the articulation of the femur, through which the weight was transferred to that bone. There is a deep notch in the wall of the acetabulum at the ilio-ischiac suture.

The ischium is carried well backward, its upper border being somewhat concave, and it seems evident that the pubis and ischium together form a wide sheet nearly at right angles to the ilium, so that they form a V-shaped trough under the tail. A very small obturator foramen passes up obliquely through the suture between the two bones; this has far more the appearance of a passage for a blood vessel than of a true obturator foramen, the short canal it encloses passing down and out vertically.

The pubis ends ventrally in a thin margin, the ischium forming a rather more massive process; their lower free borders were presumably cartilage clad. It is remarkable that their hinder borders are about at the level of the fifth or sixth caudal vertebra. It is not very easy to determine where the cloaca—if such it were—lay. But it seems likely that the hinder end of the body was quite abrupt, the tail a small, perhaps pig-like, appendage (Fig. 23B).

The femora of both sides are well preserved, and together give an excellent idea of the character of the bone. It is quite obvious that the two femora of this individual are of different lengths. They lie in position with the complete pelvis and are, beyond question, bones of the same individual, yet they differ in length by more than a quarter. It is evident that the difference existed in life, and has not been produced by crushing, for the bones lie flat on a bedding plane, so that they cannot have been distorted in any way which could have affected their

length. Such differences between right and left limbs of the same individual are not common, but are, of course, familiar enough in man.

The head of the femur is rounded (Fig. 17D and E) and projects very slightly inwards, is obviously thickly cartilage covered, and is continuous with the border of a trochanter which is a thin sheet of bone projecting laterally, widening as it passes outwards to the rounded and slightly thickened lateral border of the bone. The shaft is wide but thin for the hinder half of its length; it then widens and thickens, becoming rather square-cut and abruptly truncated by a face which may be even a little concave and must have been cartilage clad. When viewed from its broad faces the proximal end of the bone is wider than the distal.

The fact that the head of the femur is continuous with the upper surface of the trochanter implies that the freedom of movement of the femur was strictly controlled, for it would prevent any great divergence of the femur from the side of the body. Its nature suggests that the hind leg could move nearly parallel to the animal's principal plane in a mammalian manner, and could not be laterally directed as in primitive tetrapods, or even in pelycosaurs.

Comparison of both hind legs, one preserved stretched out, the other flexed, makes the structure of the knee quite evident. The articular surface of the tibia is actually hidden by matrix (Fig. 14E) but its borders show that it is triangular, gently convex, and obviously carried a good deal of articular cartilage. The bone narrows rapidly to the middle of the shaft, and then enlarges again to the abruptly truncated distal end.

The wide proximal end of the fibula is obliquely faceted for the femur, and its borders are expanded for attachment of the capsule. The posterior surface is flat and the outer surface considerably swollen. The shaft is slender, widely separated from the tibia, and ends abruptly short of that bone.

The tarsus, of which no bones are preserved, is indicated by a space in the matrix between the tibia and metatarsals, certainly little wider than its length, but nothing is known of its nature.

Three digits of the hind foot are preserved in position and show that it was a good deal smaller than the hand, not only in the length of the individual bones but especially in their slenderness. Such evidence as exists suggests that the number of phalanges was that common to mammals, and the claws when seen from below are provided with a powerful attachment for a tendon, and are of considerable length and perhaps relatively thick.

Diictodontoides skaios

The first sacral centrum is very different from the last lumbar: although the same length, it is very much shallower, the rib articulation being about 3.5 mm. above the mid ventral line, instead of at least 11.0 mm., as in the preceeding one. The centra of the three sacral vertebrae become progressively shorter and more slender. The sacral ribs are relatively massive bones, completely continuous with the centra, each with a minimum diameter of 4 mm., expanding to form a continuous joint surface 20 mm. long and at least 7 mm. high for attachment of the ilium.

The left ilium as preserved stands vertically across the bedding, the right lies on a bedding plane, they thus differ a little in shape. The right measures 30 mm. in height from the articulation with the pubis to the dorsal border, whilst the similar measurement of the left is 22.5 mm. only. I record these facts because they show that bones found buried in Karroo dust, if across the bedding, may be compressed by a quarter without showing any signs of distortion.

The pubis and ischium of the left side lie in the matrix in position with respect to one another, and are seen from below. They show the borders of the lower part of the acetabulum, which form ridges projecting round it. Their mutual suture is a flat face broken by a very narrow but antero-posteriorly elongated obturator foramen, lying as close as possible to the acetabulum. Below this the two bones are very thin, and are progressively less well ossified towards the ventral border. The pubis is exceptionally well shown, with a well defined ventral process directed downwards and outwards below the anterior border of the acetabular region. It is evident that, as in other anomodonts, the right and left sides did not meet ventrally.

The femur appears to be very different from that of the other animals in question. In it the head shows only the beginning of an inturning, and is essentially a flat area truncating the cylindroid shaft nearly transversely, clearly cartilage capped, and extended out into a very powerful trochanter, no doubt a muscle attachment, which appears also to have been cartilage clad. The implication is that in life the femur projected out laterally from the acetabulum and a little, but not much downward. If so, and the position of the bones in the matrix confirms this idea, then the knee joint must have been capable of considerable mobility. This is consistent with what we know of that joint.

The anterior border of the tibia is essentially straight whilst the hinder border of the shaft is considerably bowed inward. The distal end is abruptly truncated, wide, thin, and a little concave; it cuts across the shaft so that the posterior border lies a little below the anterior one.

The fibula, which is very imperfectly shown, is a much more slender bone, and although its full length is not available, its lower end, where broken off, is already nearly as wide as the distal end of the tibia.

In the specimen the left femur is in articulation with its tibia, but the knee joint has been considerably laterally compressed. The bones of the right side are not crushed but are much less favourably exposed. The two hind legs are symmetrically disposed, the femora passing out nearly at right angles to the animal's backbone, thus confirming the inferred pose, the lower leg being turned abruptly downward and backward, and the hind feet continuing the direction of the tibiae without marked angulation. This position seems perfectly natural and, if taken at its face value, suggests a sprawling gait, and hence a very wide track. But such a pose is not that which normally occurs in dicynodonts, nor are the shapes of the individual limb bones of *Diictodontoides* similar to those of the majority of anomodonts. The difference can only have a functional significance, and I think the implication is that the animal was very largely aquatic, swimming freely with its limbs, but no doubt capable of coming overland when necessary.

It may be noted that it does not form a possible ancestor of *Lystrosaurus*,

presumably even more committed to an aquatic life, with a very characteristic and highly specialised skull shape. But in the following respects:—depth and width of skull, distance of nostril above border of mouth, short, thick radius and ulna, broad hand with wide phalanges and short toes, it has some features which may well be associated with life in water, and are to some small degree reminiscent of those found in *Lystrosaurus*.

The right tarsus is well preserved, although it is not easy to make out its structure, because it is to some extent curled on itself so that the toes lie in a position difficult to prepare and to interpret. The left hind foot is shown more comprehensively so far as its phalanges and metapodials are concerned, but the tarsus is less well preserved. In the right foot four tarsal elements are visible, two well finished proximal ones and two more nodular distal ones. The proximal row contains two bones, presumably a tibiale and a fibulare (calcaneum), and these differ very considerably. The fibulare is a rather large, approximately rectangular bone of considerable thickness, which evidently articulated in a manner not now comprehensible with the very much smaller tibiale, whose proximal articular face, wide, deep and much rounded, suggests the possibility of very considerable movement of the foot on the lower leg, including in all probability an approach to flexure through more than a right angle. The fibulare would also allow of a good deal of flexure proximally and at its distal border. The fibulare of the right foot is in evident articulation with a distal tarsal which appears not to be a centrale, and this bone is itself in contact with another distal tarsal and with the tibiale.

The metatarsals are shown in both hind feet. In the right foot they are not very intelligible, but in the left foot four of them are well shown. The first is a curious element not looking like an ordinary metatarsal, for it is effectively quadrangular in plan. The three which can be seen lying lateral to it have short shafts with somewhat enlarged heads and distal extremities. Their proximal ends meet, and the foot is quite wide. Proximal phalanges of four of the digits are quite well shown, and enough remains of the distal phalanges to justify Fig. 14G.

FOOTPRINTS

The study of fossil footprints has a long history from the first description of *Cheirotherium* to Hickling's account (1909), where he provides an "atlas" which brings together, not only all the Permian tracks of Britain, but others from Permian and Carboniferous rocks abroad with which he compares them.

The distribution of fossil footprints is extraordinarily erratic. Of those which may reasonably be regarded as dicynodont—by virtue of the long, forwardly pointing third finger, and width between opposite prints—only one series (a line of three sets of claw marks with traces of another print) has been found in the Cutties Hillock beds of Elgin, which actually contain the dicynodont *Gordonia*, though at a somewhat lower level; but tracks are abundant at Cummingstone, five miles away, where no fossil bones have been found.

An even more extreme case is that although hundreds of *Cheirotherium* footprints have been found in Britain and Germany, no trace of a bone of the animal which made them has ever been discovered there, the only evidence as to its nature coming from South America, where there are no tracks!

The Cummingstone tracks are of a kind shown by Hickling to be the most abundant of Upper Permian footprints in Britain, others of which come from Exeter, Mansfield, Penrith and Dumfries and have been described by various authors; they are well summarised and figured by Hickling as "Chelichnid forms." There is also one specimen showing fore and hind footprints of a track from Middelburg, South Africa, now in Munich, figured by Seeley (1904). From the figures this track seems not to be dicynodont, the fact that the fifth digit in both fore and hind feet is very long being a noticeable difference. It has more nearly the appearance of a lizard-like reptile. No others which could be attributed to dicynodonts are known.

A slab which I found at Middelburgh, C.P., R.321, showing six associated prints (Plate 1), is therefore of interest. It comes from the summit of the Cistecephalus zone, or the base of the Lystrosaurus zone, and is thus, with the Munich specimen, the only one known from the Karroo system. It is a track showing impressions of right and left fore and hind feet, which are five-fingered and five-toed respectively and noticeably different in size, the fore feet being considerably larger than the hind. The animal was clearly plantigrade, the palm of the hand and the sole of the foot showing no continuation of the division into fingers or toes. These are short, the third digit is the longest and directed forward, the others being rather symmetrically placed round it. The track is comparatively wide, the footprints of opposite sides being separated by about the width of a fore foot print. A tail streak—a smooth, shallow groove with a raised rib running along the middle of its length—shows between the central pair of prints.

This track does not agree with any of those figured by Hickling. It was made by an animal with a tail long enough to reach the ground occasionally during normal walking, but the chief difference is the very wide separation of individual prints of fore and hind feet in it; two prints made by the same foot are separated from one another by nearly four times their own length; and the fore foot print lies exactly half way between two prints of the same hind foot, a condition not often seen in recorded tracks. In the imprint of the tracks figured by Hickling fore and hind footprints commonly overlap one another, a very different pattern, dependent, however, on so many different body qualities as to be incapable of satisfactory analysis.

Nevertheless, in spite of these differences, both kinds of track could in principle be dicynodont. They are certainly not amphibian or sauropsid, and are probably not gorgonopsid or cynodont.

The track of R.321 could not have been made by any of the specimens described in this paper; it does not conform in size, being too big for the three small anomodonts, and too small for *D. halli*, and the existence of a tail-streak implies a tail at least long enough to reach the ground.

The footprints which can perhaps be referred to *Dicynodon* agree in showing no sign whatsoever of scales on the sole of the foot, which are sometimes visible in, for instance, the pseudosuchian *Cheirotherium*.

TUSKS

In the remarkable paper in which he first described *Dicynodon*, Richard Owen (1845) discussed the nature of the canine tusks of that animal in much detail. He recognised the existence of a very thin coat of enamel, showed the extent to which the tooth is lodged in its socket, and described the histology of the tooth. Then he considered its use, noting that in the type skull of *D. lacerticeps* the "canine is sharp pointed, showing no sign of any obliquely bevelled or chisel-shaped extremity which is produced by habitual application in the acts of obtaining daily food, as for example in the protruded extremities of the tusks of the dugong, and the incisors of rodents . . . I conclude, therefore, from their shape, proportional length, sharp points and dense texture, that the tusks of *Dicynodon* were applied by the living animal either for the purpose of killing its prey, or defending itself from its foes, or in both acts; and that they were offensive and defensive arms."

Owen had recognised that both upper and lower jaws of *Dicynodon* carried a tortoise-like horny beak, but he did not then know of the existence of *Oudenodon*, where in the absence of a canine only the horn-covered jaw could have been used to collect as well as to masticate food. Later (1860) he named *Oudenodon*, recognising that it might prove to be only a female *Dicynodon*, but in the absence of closely similar specimens, some tusked and some not, retained the generic name. Thus it remained for long uncertain what was the relationship between the two forms: even yet there are very few cases in which tusked and tuskless animals, clearly of the same species, have been found. In any case it is evident that the oudenodont condition enabled an animal as large as any *Dicynodon* to collect adequate food, and that the tusk is therefore no essential part of the feeding mechanism.

The tusks were, thus, not used in day to day life, and it is interesting to see if they show signs of wear, and if so in what way.

DICYNODON BOLORHINOIDES SP. NOV.

The skull illustrated in Figs. 18 and 19, R.519, belongs to a new species which I name here as *Dicynodon bolorhinoides*. It comes from the upper part of the Endothiodon or Lower Cistecephalus zone of Kuilspoort, near Beaufort West, C.P. and is 27.5 cm. in length. *D. bolorhinus* Broom is perhaps the nearest to it, but my specimen differs because the nasals meet between the premaxillae and frontals, and there is more space between the nasal and orbital openings. It also bears resemblances to *D. halli*, but the postfrontals are not comparable, the snout is wider, and the interorbital width bigger. The bosses over the nostrils are characteristic, not occurring in the same form in any figure of a dicynodont skull I have been able to examine.

One structure exceptionally well shown in the specimen is the relation of the lower jaw to the skull. The narrow anterior part of the fused dentaries is held between the inner sides of the tusks, fitting very accurately. Indeed it is evident that, with the covering of horny beak replaced, there can have been extremely

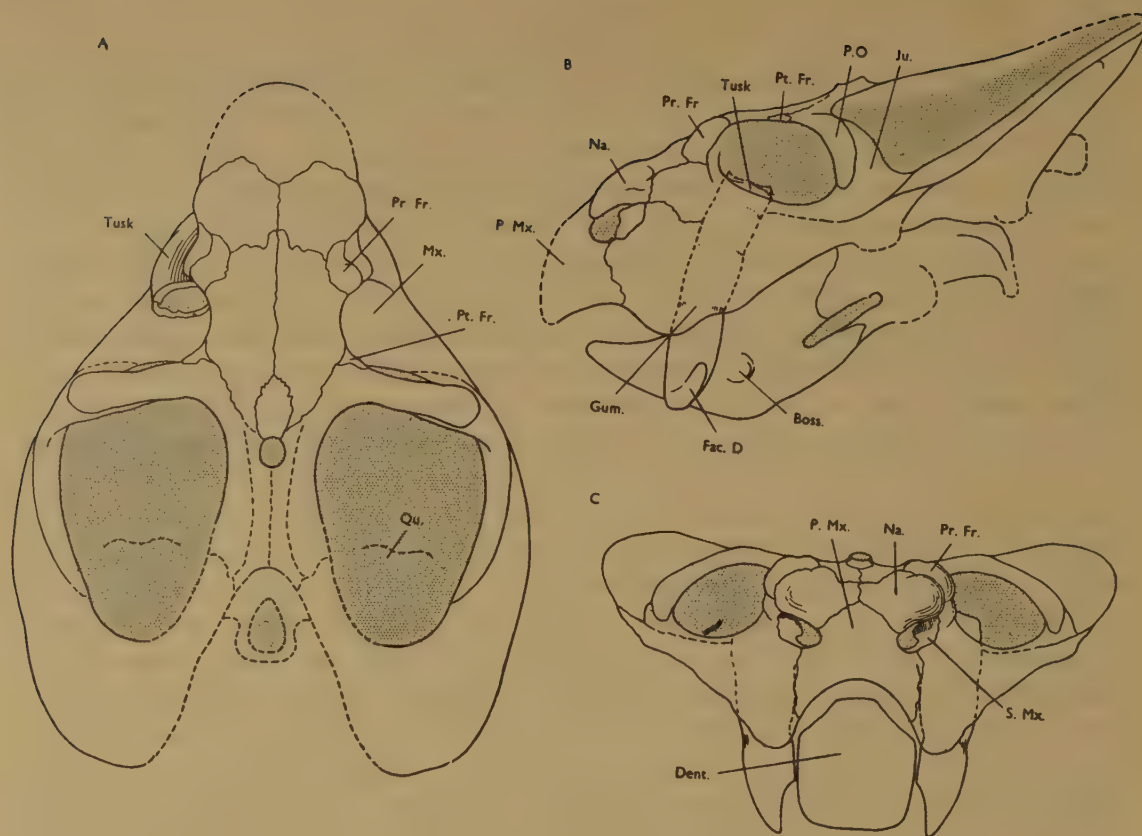


Fig. 18. *Dicynodon bolorhinoides*, sp. nov., R.519, Upper Endothiodon or Lower Cistecephalus zone, Kuilspoort, Beaufort West, C.P. $\times \frac{1}{3}$.

The specimen, which appears to be uncrushed, has received very little deliberate preparation; the bone was exposed by natural fractures, which often followed its surface, and make much evident—even of the internal anatomy. The tusks of both sides (Fig. 19) were pushed up into the orbits after death, so that their roots are visible (as shown in the drawing); the maxilla is stripped from the left tusk so that it is fully exposed (and can be lifted out of its present socket); the right is still covered by bone, and its root partly concealed by matrix. The distance by which the tusk has been pushed up in its socket is shown by the position of the constricted band (Gum) above the border of the maxilla.

A, the skull from above; B, from its left side, with the lower jaw in its extreme forward position, and the mouth nearly closed, so that the upper border of the dentary is mostly concealed by the lower border of the maxilla; C, from in front; there is a narrow space between the dentary and the tusk for the lateral part of the horny beak of the lower jaw, the width of this space is the difference between direct measurements of the width of the lower jaw, and the distance between the inner sides of the tusks; it is evident that the orbits are so placed that stereoscopic vision is possible: how far this condition is general cannot be indicated, because I know of no other figure of a dicynodont skull viewed directly from in front.

Boss, boss causing wear facet *b*, (see Fig. 19); Fac.D., wear facet on the external surface of the left tusk labelled *d*, in Fig. 19.; Gum, the depressed ring in the root of the canine tooth which marks the place where the tooth was held in position by gum; Ju. jugal; Mx., floor of the orbit formed by the maxilla which in life covers the root of the tusk; Tusk, left canine tusk slightly displaced in orbit. (Key to other abbreviations p. 206.)

little lateral play of the lower jaw when the mouth was closed, a matter which emphasises the effectiveness of the antero-posterior movement made possible in dicynodonts by the structure of the quadrate/articular joint.

The great posterior extension of the squamosal implies that the temporal muscle was long, and therefore capable of considerable lengthening, which would enable the mouth to be opened very widely, thus clearing the tusk.

This skull has perfectly preserved tusks, untouched by any tool, the left one of which falls out of (and can be replaced in) its socket in the maxilla, the bone covering it having weathered away. The left tooth lies in position (Fig. 18B) but has been driven upwards so that, as shown in the drawing, the root lies in the orbit. The root is still covered with the exceedingly thin bone of the orbital wall which it has forced upwards.

On both tusks a definite constriction (Gum.) occurs at the base of the exerted part of the tooth. It takes the form of a shallow groove, with sharply defined borders, which runs most markedly round the posterior and lateral surfaces, but is shown less clearly marked on the admesial surface. This evidently represents

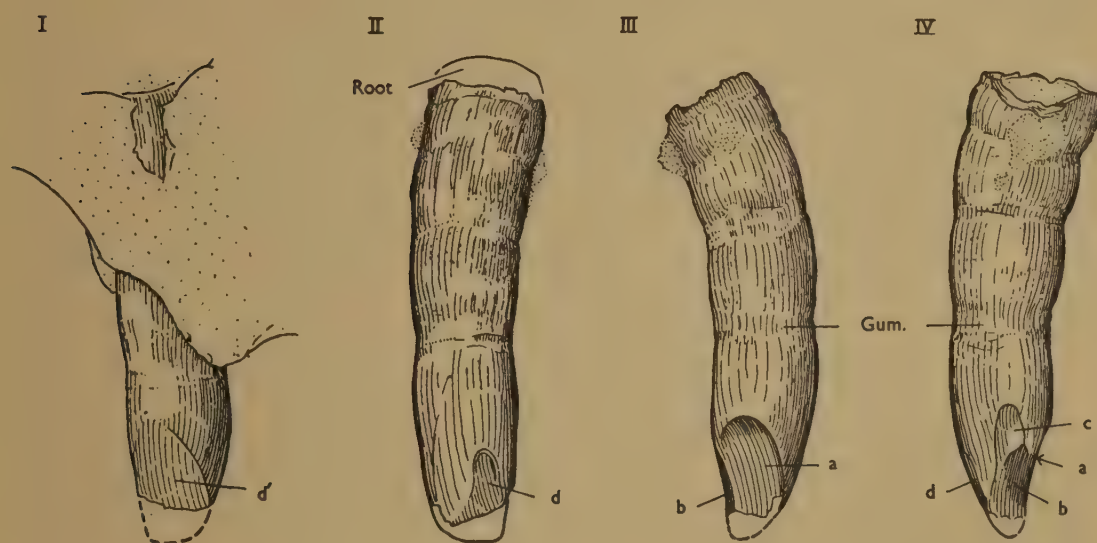


Fig. 19. *Dicynodon bolorhinoides*, sp. nov., R.519, Upper Endothiodon or Lower Cistecephalus zone, Kuilspoort, Beaufort West, C.P. $\times \frac{2}{3}$.

I, right tusk in position, from the outside; the area covered by widely spaced dots is the maxilla; the tusk shows at d', the wear facet made by abrasion by vegetation; II, III and IV, the left tusk taken out of its seating in the specimen (Fig. 18); II, outer surface; the tip of the tooth is restored from an impression in the matrix; the unshaded area at the root represents part of the infilling of the pulp cavity and gives its full length; d, is the wear facet equivalent to d'; III, inner surface, showing a, the facet worn by contact with the lower beak, b, that made by the boss on the dentary; IV, posterior surface, a, surface worn by contact with side of lower beak, b, and c, facets made by the boss on the dentary, d, external abrasions.

Gum, the groove made by the gum which surrounds the tooth.

the point where the tooth emerges from the soft tissues of the upper jaw. All above it is root, and the two further rings on this part of the tooth may have served to secure its firm implantation in the socket, from which it is separated by a very small space; or they may possibly represent regions of the tusk laid down at different periods of life showing variation in the available food supply, or some similar unpredictable occurrence.

R.443, with a skull length of about 5.6 cm., has a left canine in position in the skull in the process of cutting. It has experienced no wear whatsoever. The tip of the crown is a rich dark brown in colour, and seems to be essentially uncracked, whilst the evident dentine lying 2.5 mm. above it is light brown in colour, considerably longitudinally cracked, and has a surface definitely rougher than that of the tip. The appearance, in fact, suggests that there was an excessively thin layer of enamel covering the extreme tip. The right canine of the same individual is less well preserved, but its admesial surface, which can be seen still plunging into matrix, also seems to have a black, excessively thin surface layer of the kind which may well be enamel.

Large tusks, such as those of *D. bolorhinoides*, seem always to lack enamel. The inner surface of the crown is worn parallel to the animal's mid plane into a facet (a) (Fig. 19, III & IV) which is flat antero-posteriorly but very slightly curved from top to bottom. The facet cuts the tooth surface abruptly and was evidently made by wear against the horny beak of the lower jaw. This antero-posterior wear facet meets an independent facet (b) on the hinder surface of the tooth at about 120 degrees, the ridge between them being rounded off over a width of less than 2 mm. The left tooth, but not the right, has a continuation (c) of this facet which is separated by a definite angle, and extends up the hinder side of the tooth for a total distance of some 2.5 cm. The wear on the inner and posterior surface implies that the beak of the lower jaw was relatively large, extending down from the upper border of the dentary for most of its depth, an arrangement particularly noticeable because the posterior wear facets (b, and c,) are caused by that part of the horny beak which covers a boss, projecting outward for about a centimetre, which was both thick and rigid. The impression of the extreme tip of the left canine is preserved, showing that the wear facets extended to it and there formed a rounded, worn and narrow end. Finally the whole visible outer surface beyond the gum is smoothed and polished with considerable wear, which to the hinder side of the left tooth includes the definite rather flattened facet (d), whilst in the right tooth the equivalent facet (d') is much wider and meets the general anterior surface at a quite definite edge. In front of, and behind, this facet both teeth are unworn.

This evidence of wear throws light on the animal's habits.

The general nature of the wear on the external surface of these teeth seems to imply the presence of masses of dust covered vegetation, close to the ground and probably reaching well above it, into which the animal thrust its head whilst feeding. *Diaelurodon*, a much smaller animal, stands only some four inches off the ground, and could not well rear up more than, say, eight inches. It could not in all probability pull anything down with its forefoot, and was therefore dependent on low growing plants. The polish on the surface of the tusks of *D. bolorhinoides*

might well be the result of abrasion by such low growing vegetation.

The backwards and forwards motion of the lower jaw with respect to the upper may have had the following functions. It could have enabled the animal to hook the premaxillary beak into a plant, and then to force its lower beak forward, scooping out a large piece of plant to be further crushed by backwards and forwards motions of the lower jaw, with the food mass firmly held between palate and jaw. Or the lower jaw at its furthest forward position could give a powerful edge to edge bite against the upper beak, which would allow the animal to chop off any protruding piece of a plant. The massiveness of all parts of the jaw apparatus, and the great space housing masticatory muscles, are the most impressive qualities of an anomodont head, scarcely to be matched in any other vertebrate. They seem to me to imply a vegetation in its physical qualities quite unlike that now found in grass covered prairies, and perhaps more similar to that present today in the Karroo—small woody bushes, and interspaced succulents with massive, water containing leaves, branches, or even bulbs. Such a diet, of a flora not yet known by actual fossil plants, may well have been available in the Karroo during the laying down of the lower zones of the Beaufort Beds. Comparison with the White River Oligocene of Dakota shows that rocks of such "plains" origin may well lack any trace of vegetation, except pieces of silicified wood, as do the Beaufort Beds. In essence such conditions still exist in much of South Africa, and indeed in inland prairie regions of North and South America, and no doubt in Siberia and China, and they are to be found in much of Australia.

The existence of these well marked surfaces of wear on the teeth of *D. bolorhinoides* described above, lead one to see if similar wear facets are to be found on other dicynodont teeth. R.262 is the front part of a small dicynodont skull some 8 cm. in length, without a lower jaw, somewhat distorted but otherwise well preserved. It retains two very well preserved canine teeth which show a wear surface on the inner side facing the lower jaw, reaching up to the level to which the maxilla extends on the front side of the tooth, and leaving a considerable region of the base of the tusk unworn. The wear surface, the equivalent of facet (a) in *D. bolorhinoides*, is very nearly flat from above down, and back to front, those of opposite sides seem evidently parallel to one another and to the mid line. It may be added that the outer surface of the left canine tooth, where it is broken off near its tip, shows a depressed area whose margin is rounded off into the general smooth external surface. This possibly represents the place where a flake has been driven off the surface of the tooth by some accident during life, the surface having then been worn smooth by the abrasive action of its surroundings. None of the other facets of *D. bolorhinoides* is represented.

The small skulls R.264, 6.4 cm. in length, and R.516, 6.0 cm. in length, have tusks with no wear facets visible.

THE DIET OF EARLY LAND VERTEBRATES

Anomodonts form the first complex assemblage of vertebrates to take to a

vegetarian diet as a group, though the tapinocephaloid *Deinocephalia* and the diadectids perhaps in part anticipated them. Previously, with a few isolated exceptions, land animals which did not eat fish, or prey on their fellows, must have lived on some form of invertebrate food, such as insects or molluscs; their teeth show that they could not have tackled plant food directly. Large land living invertebrates, which would have provided a perfectly adequate diet for even a big animal, existed in Carboniferous and early Permian times, and they were probably there in requisite numbers. There was also a flora adequate to sustain the invertebrates.

Devonian

No land vertebrates are, of course, known for the Lower and Middle Devonian of any part of the world, and their absence presumably implies that the amphibia had not by then come into existence.

A consideration of the possible diet of the first vertebrates known to inhabit the land, the *Ichthyostegalia* from the Upper Old Red Sandstone of Greenland, shows that they were ill-fitted for eating plants. They have a marginal dentition of close-set small teeth like those of later labyrinthodonts, and palatal tusks of larger size, and were well fitted for catching and eating fish during their time in water.

Carboniferous

The next amphibian fauna is found in the Burdiehouse Limestone of the Edinburgh district, and in other rocks of about the same age. The age of these rocks in a standard succession of Carboniferous times is not very certainly understood, but the Burdiehouse Limestone, at any rate, seems to be Mississippian in a world sense. Thus *Otocratia* from this horizon (whose systematic position is still uncertain), and *Pholidogaster* from the Gilmerton Ironstone, are still regarded as being of Mississippian age, together with *Dolichopareias* and *Adelogyrinus*. Most other Lower Carboniferous amphibia from Scotland, which I described in 1929, are Namurian. All these forms are evidently not herbivorous.

In the Upper Carboniferous occurs *Eugyrinus wildi*, the only known form from the Lower Coal Measures, the type specimen of which actually retains the four wings of an insect in the position of its stomach (Watson, 1940, p. 217), although it was washed out to sea, and found with cephalopod shells in a shale of marine origin. Thus it evidently was insectivorous in adult as well as in larval stages.

Insects are only preserved as fossils in exceptional circumstances, and we know relatively little about their early history in Silurian and Devonian times; Neuroptera and Hemiptera are, however, recorded then. In any case we may almost take it for granted that the effective feeding phase of all primitive insects must have been based on plant eating; there was probably very little else directly available. Furthermore, although the actual number of palaeozoic insects known is small, and they are peculiarly difficult of preservation, such casual observations as the

common occurrence, in sections of coal balls of Upper Carboniferous age, of what are evidently insect burrows in wood, suggests that they played an important and varied part in that day, filling, perhaps, much of the rôle of intermediate between plant and carnivorous animal, which in Tertiary times was largely occupied by herbivorous mammals, belonging to many orders, whose individuals varied enormously in size.

Later in the Carboniferous amphibia belonging not only to labyrinthodonts, but to other groups, became abundant, and have been described from the Coal Measures of Scotland, England, Ireland, Czechoslovakia, and the U.S.A. It seems impracticable to discuss the food habits of these creatures, other than to point out that none shows clear signs of being fitted for plant eating. There is little direct evidence; and even specialised dentitions, such as that of *Batrachiderpeton lineatum* (Watson, 1913), are very difficult to interpret in terms of function, though the latter does show an unusual quality in the presence of a mass of small, almost granular teeth, covering the whole mid-region of the pterygoid across the middle line, surrounded by longer teeth in the vomers and palatines. The whole curious arrangement lies entirely posterior to the small group of marginal teeth in the premaxilla and maxilla. This dentition seems quite inappropriate to plant eating, though it is difficult to point to an exact parallel in any other animal. It seems suitable to deal with invertebrates which require to be crushed before being swallowed.

It is evident that large Upper Carboniferous amphibia such as *Loxomma* lived on fish, to whose capture their dentition is completely suited, and which, in great numbers, are always found associated with them in the shales, like those at Newsham, from which they come.

In Carboniferous times it is thus evident that the most advanced animals—such amphibia as are yet known—did not directly eat plants. If the food chains of which they were the summit followed a probable course, it seems likely that the first members which ate plants directly were invertebrates, and that this pattern survived until, with dicynodonts, faunas appeared in which the dominant carnivores were able to live on plant-eating relatives, as do mammals.

Therefore it seems as if herbivorous vertebrates arose at some time after the Coal Measures. It may be noted, however, that a cycadofilician plant of the Lower and Middle Coal Measures, *Trigonocarpus*, had a seed combining a fleshy outer coat with a very hard inner seed coat, which in turn housed a nucellus, the summit of which was a pollen chamber of essentially cycadian pattern. The existence of the fleshy seed coat implies that the fruit was attractive to something: it may have been so to an insect conveying pollen, or eating the fruit, though this would hardly help in its dispersal, but it is also possible that it was tempting to a herbivorous vertebrate which would have conveyed the seed away from the parent plant.* There is, however, no evidence of the existence of herbivorous tetrapods at that time, and it is reasonable to suppose that, had they occurred,

*Sir Edward Salisbury tells me that the fleshy covering of the maidenhair tree's fruit has no attraction at all to the human palate, and with decay becomes extremely unpleasant to taste, but whether animals enjoy it is not known.

some specimens would have been found, since—on the analogy of fossil mammals—vegetarians greatly outnumber carnivores.

Early Permian—Texas

In the basal Permian Red Beds fauna of Texas we find for the first time, in such reptiles as *Diadectes*, *Captorhinus*, and *Edaphosaurus*, a dentition capable of crushing plant food. And Romer (1940) believes that *Casea*, which appears later, was also a herbivore. Indeed, except in extreme cases such as placodonts, sea otters, and perhaps Dipnoi, does a crushing dentition ever have another function? It is most difficult to judge the possibility.

Diadectes has a dentition which often shows signs of heavy wear, and seems designed to take into the mouth and grind up plants (Watson, 1954, p. 439), thus, with *Edaphosaurus*, it is probably the oldest vegetarian vertebrate. But it is rare, compared with the carnivorous *Dimetrodon*, for instance, in contrast to the great preponderance of dicynodonts in all South African Permian faunas.

Captorhinus, with a skull length of some 7 cm., has a strip about 2.5 cm. by 0.5 cm. covered with a patch of small cylindroid teeth, a little more than a millimetre in diameter, on each side of the upper and lower jaws. Such a device is probably better adapted to plant than to animal food, though it does not seem well developed for either purpose. The articulation of the lower jaw with the quadrate condyle is one which leaves it freely moveable over a considerable range, with the mouth open or closed, and this condition (which is effectively that found in *Testudo*) is presumably also much more suited to a plant than an animal diet. It must be remembered, however, that the jaw articulation of *Dimetrodon*, an obvious carnivore, allows of a considerable antero-posterior slide of the articular on the quadrate, analogous to that of *Captorhinus*.

Romer & Price (1940) discuss the food habits of *Edaphosaurus*, in which the pterygoid is thickened orally and studded with close-set granulations of teeth of a considerable size, which bite against a correspondingly toothed plate in the lower jaw. They conclude, obviously correctly, that the animal was herbivorous, and not, as an earlier author had suggested, a devourer of molluscs.

Thus, the Texan Red Beds of Lower Permian age were laid down on a land inhabited by herbivorous reptiles. But strangely enough these are very much rarer than the carnivorous pelycosaurs found with them, a condition which is not expected, and which cannot be paralleled in land faunas of any subsequent age, except perhaps in rare cases, such as that found in hyaena caves. The explanation of this remarkable fact may be that the earliest reptiles were derived from carnivorous amphibia, and were thus themselves carnivorous, and that they preyed largely on the amphibia, which in turn lived mainly on fish.

The Texan Red Beds grade upward into much less fossiliferous rocks, in which Olson (1958) has shown that the normal Texan Permian fauna continues with slight modification, represented, however, by very rare materials.

Permian—Urals

The next fauna is found, not in America, but in Russia, in the Copper Mines of Orenburg, towards the Urals. It contains therapsids, evidently in effect pelycosaur descendants, but of advanced structure in the head and limbs, and some plants associated with them. Amongst them is the first tapinocephaloid, *Deuterosaurus*, which retains massive canines, and has very large incisor teeth with a projecting cusp on the outer surface of the crown, and an inwardly directed, basin-shaped heel. The upper and lower teeth interlock, so that their heels form an effective crushing mechanism whose workings are shown by the wear facets (Efremov, 1954, figs. 17 and 23). This must be a herbivorous dentition. It may be very differently developed in different members of the group, and the teeth may, indeed, in such later forms as *Mormosaurus*, be reduced almost to mere pegs. The group reaches its maximum in later Middle Permian deposits (Isheyvo) in Russia, where plants are hardly known, appears as giant forms in the Tapinocephalus zone of South Africa, and then vanishes.

From the time of their first appearance in the Urals tapinocephaloids in Russia are associated with a close relative, *Venjukovia*, which provides a nearly perfect ancestor for the anomodonts. It shows the beginning of the secondary palate, and has a premaxillary dentition with large, chisel-like teeth (suitable for cutting into plants) which bite against the anterior teeth of the lower jaw, producing large wear facets on them. Behind these are small maxillary teeth, followed by an enlarged—but still not impressive—upper canine, and this in turn is followed by five small teeth with blunted crowns. The canine and maxillary teeth behind it bite against a lateral projection from the dentary, which bears a series of shallow depressions into which they fit, and hence must have been covered by a horny sheet, the primordium of *Dicynodon*'s beak. From this the step to the endothyrid condition is a small one, though obscured by the development in endothyrids of feeding habits which required a battery of slender, saw-edged teeth in the jaws, to shred plants into strips after they had been taken into the mouth. Finally, the full development of the horny beak, a most efficient cutting mechanism, rendered such devices unnecessary, and led directly to the later Anomodontia. It may be noted that *Dicynodon* proper is not found in the Ural, or the Isheyvo, Permian faunas, an indication that the Tapinocephalus zone of South Africa, where it first occurs, is later in time.

*Permian—South Africa**Tapinocephalus zone*

There are three sets of undoubtedly herbivorous reptiles—but no plants, except wood—known in the Tapinocephalus zone of South Africa.

The members of one group—the pareiasaurs—are very large and heavily built. They have a feeble, continuous row of teeth whose axes are directed in towards the cavity of the mouth, each tooth having a flattened crown cut into a series of

blunt points. There are also patches of backwardly directed, small, pointed teeth on the roof of the mouth. The jaw articulation is a fixed hinge. The marginal teeth show no signs of any specialised function, and would merely control a mass of plant food taken into the mouth (such as water weed: though there is nothing about the postcranial skeleton to suggest an aquatic life). These teeth are so small, and of such a character, that they were unlikely to be capable of biting a piece out of a massive plant, and hence pareiasaurs cannot be counted as vegetarians in the sense that the anomodonts are.

The next group—the tapinocephaloids—in general agree with their ancestor, *Deuterosaurus*, in the character of the teeth. They are vegetarians of enormous size, are rather rare as fossils, and evidently scarcely competed with the anomodonts; in any case they died out at the end of Tapinocephalus times.

The third group—the anomodonts proper, endothiodonts as well as dicynodonts—found at the top of the Tapinocephalus zone, but not in association with pareiasaurs, are relatively few and small. They have been described by Broom (1905a) and others, and include the skull sectioned by the Sollases (1913). *Brachyprosopus*, a new genus described by Olson (1937), is a very typical form retaining a rather larger group of maxillary teeth than usual, in a skull which otherwise has the normal dicynodont horny beak. It is therefore evident that by the time of this zone a typical dicynodont structure had been achieved, to remain without fundamental modification until the disappearance of the group some time in the Trias. An analysis of the jaw mechanism, and wear on teeth, will show that plant food is all that later dicynodonts could have tackled, and there is a convincing series of stages showing the gradual loss of individual teeth and development of the characteristic beak. Canine teeth may survive in dicynodonts up to the time of the disappearance of the group; but the occurrence of *Oudenodon*—distinguishable from *Dicynodon* only by its lack of canines—over the Permian part of the whole range, suggests that the canine, often a huge structure showing wear facets, was, none the less, not an essential part of the feeding mechanism.

These three different types of dentition, though all herbivorous, imply differing food habits, but in the practically complete absence of any knowledge of the plants amongst which the animals lived, little can usefully be said as to their precise functional significance.

Endothiodon zone

In the Endothiodon zone the tapinocephaloids do not occur, having become extinct, and pareiasaurs become very much rarer. Dicynodonts go on, but the most striking occurrence is the great increase in the number of endothiodonts, which include some giant forms. These are seldom found in close association with dicynodonts, indeed, I think, never with any large form of that genus.

Endothiodonts have certain characters, common to all the large forms, which distinguish them from dicynodonts. For example, in such giants as *Endothiodon* and *Esoterodon*, the face is characteristic in having no trace of a canine tooth, nor even of any downward projection which would recall its former presence. This is well shown in the side views of skulls of *Endothiodon bathystoma* and *Esoterodon uniseries*, figured by Broom (1905a). On the other hand many of the small

endothiodonts do retain a canine tooth, embedded in a process of the maxilla, like that of dicynodonts, and the process may remain after the canines cease to be formed, as for example in *Opisthoctenodon*. These facts seem to confirm that the canine is not used in feeding. Thus, in this zone, the competition for food was essentially between dicynodonts and endothiodonts.

Cistecephalus zone

In the *Cistecephalus* zone pareiasaurs continue, rare in South Africa, abundantly represented in Russia. Endothiodonts vanish, and dicynodonts become very much commoner, and larger. They become, indeed, a dominant group, and include animals of all sizes from a mouse to a hippopotamus, forming an enormous plains fauna, and providing food for a great variety of carnivores, which are found, however, in far smaller numbers.* They show little change in morphology, though the very large forms have relatively larger muscle insertions than the small, shown usually in relative increase in size of the squamosals.

Lystrosaurus zone

The changed conditions of the *Lystrosaurus* zone abruptly removed dicynodonts from the Karroo, leaving the aquatic *Lystrosaurus* to represent the group.

With the *Cynognathus* zone dicynodonts reappear in the form of *Kannemeyeria*, of which no small individuals are known, though they must have existed in youth. The only indication of the presence of other anomodonts is given by an imperfect scapula from Lady Frere, R.491, which is anomodont, but evidently not *Kannemeyeria*, and—in the Manda Beds of East Africa—*Dicynodon njalilus*, which comes from a higher horizon than *Kannemeyeria*.

Triassic dicynodonts of large size and later date are known in South America and China.

GROWTH

One trouble in all discussions of faunas of which anomodonts are members is our ignorance of the nature of the life history and individual growth of these forms. Do they grow indefinitely throughout life, as reptiles in general do? Or are they like mammals or birds, forms with a fixed maximum size attained after a youthful growing period, which comes to an end relatively early in the animal's normal expectation of life?

Tooth change

The best evidence we could hope to get is that which could be derived from the tooth change. It is evident that if an animal grows larger it must change its

*I possess a large dicynodont humerus from the *Cistecephalus* zone of Thabanchu, O.F.S., R.280, which has a hole of nearly circular section through the bone. This contains matrix full of bone fragments, presumably made by the bite of a carnivore, whether before or after death cannot be stated.

teeth, so that even in the oldest and largest individual they are competent to enable it to get a living. Thus, indefinite continuous tooth replacement, like that of living lizards, should occur in therapsids, unless growth were limited as in mammals.

In the case of *Gorgonopsia* and *Therocephalia* Kermack (1956) has shown quite clearly that tooth change occurs only once, but in pelycosaurs it seems to be quite indefinite. Toerien (1953) gives a drawing representing a section through the maxilla of a very small specimen of *D. vanderhorsti*, showing a canine tooth with a capacious pulp cavity in use, and what is evidently a successor, uncut in the maxilla, its root immediately in front of the orbit; but he found no such condition existing in large individuals where suitable cuts had been made. This is, perhaps, the most satisfactory evidence yet adduced to show that the dicynodont canine, in one form at least, had a milk predecessor. Endothiodont material often suggests tooth change in progress (Watson, 1948, p. 846, Fig. 9), though these skulls usually have the lower jaw in position and are in a hard matrix, so that the evidence concerning tooth change is difficult to investigate. It is possible that acid preparations of more of them may make the whole story clear. The appearance of the banks of teeth in such an animal as *E. bathystoma*, however, is more consistent with a continuous replacement throughout life, than of a single series surviving unreplaced.

Dicynodon itself, and *Lystrosaurus*, either have no teeth, or have canine tusks only. There is some evidence that the tusks were replaced, but the horny beak clearly was not—it grew continuously, and the bone on which it was moulded records only its character at the time of the animal's death. The beak itself is never preserved, nor in fact does it leave any evidence in the matrix of its former extent. This is true also of *Chelonia*, which afford a parallel.

Thus, it is impossible to determine on the evidence of tooth change whether or not an anomodont skull has achieved the normal adult size of its species. But the teeth may show that the individual is juvenile, as in *D. pygmaeus*, R.443, where signs of youth are the unerupted tusks, short nose, and shallow skull. And the condition of the tusk of *D. bolorhinoides*, R.519, is surely an indication that the individual was old, so that in this specimen the teeth can give some indication of age, evidence which deserves looking for in other specimens.

Sutures between skull bones

In a mammal the closure of the sutures between the membrane bones of the skull marks the attainment of its full growth. But in dicynodont skulls the corresponding sutures seem never to fuse, except for the very early anastomosis between the dentaries, the splenials, the premaxillae,* and the cartilaginous bones of the braincase. Any skull in which the dentaries are not fused is certainly

*In *Diaelurodon* R.451 the existence of an open suture between the premaxillae is made evident by the fact that the two bones have moved with respect to one another, so that their palatal surfaces are not continuous, that on the left being depressed below the right side.

that of a very young individual.

In R.315, maximum length 2.9 cm., the smallest anomodont skull I know (Fig. 21A and B), a suture between the dentaries is evident, and this specimen must be an exceedingly young individual because not only is it very small, but the fact that it has squashed flat in the nodule, without breaking or distortion, shows that the bones, especially of the braincase, must have been lightly ossified, and the sutures not closed. The premaxillae seem to be already fused.

In young skulls sutures tend to be smooth, while in old ones they are interdigitated.

Thus, the information as to individual age which can be derived from the nature of the sutures between skull bones is exceedingly slender. The literature about dicynodonts includes many figures in which the sutural pattern of the skull bones is incompletely, often not at all, shown, the suggestion being that they had fused with one another. I am very doubtful whether any such conclusion is justified: certain sutures did fuse, but, none the less, remain visible in sufficient specimens to make it evident that the bones in question are paired.

On the whole South African fossil reptile skulls show the sutures very well, and these, apart from the fusions previously mentioned, though sometimes difficult to observe, seem to me to remain open throughout life, implying an indefinite growth period.

Postcranial region

In animals in which growth ceases, i.e. in mammals and birds, it is commonly found that bones which do not move on one another in the course of ordinary living activities fuse with one another; the most familiar examples are the bones surrounding the brain—parietals, frontals, and the braincase in general—which fuse when growth ceases. Similarly the bones of the pelvis fuse in these two groups.

In dicynodonts no such fusion occurs in pelvis or shoulder girdle: even in the gigantic scapulo-coracoid, R.498, described above (p. 163), where, if the proportions of shoulder girdle to head were as in *D. halli* the skull would have been 71 cm. long, the glenoid cavity was still lined with cartilage, apparently proportionately as thick as in *D. halli*, and the three bones have moved with respect to one another, so that strips of matrix clearly separate them (Fig. 20).

Such a condition raises many points for discussion. One obvious problem is whether growth slows down gently as the animal gets bigger, but continues until the animal's death. Another is whether fusions between neighbouring bones do eventually occur, thus altering the nature of any future growth. It is evidently impossible to determine such matters with certainty, but examination of a range of material may allow one to reach probable conclusions.

The limitation of growth in mammalian limbs is marked by the fusion of the epiphyses with the shafts of the bones. No dicynodont, and so far as I know no therapsid, possesses epiphyses, or shows any indication of how those structures arose. The natural assumption is that growth in these forms was unlimited until the death of the animal. The existence of this reptilian condition is, of course,

not capable of complete establishment in fossil material, but the occurrence of gigantic limb bones, obviously still possessing cartilaginous extremities, makes it effectively certain that such was the condition in anomodonts.

However, one fact which is very noticeable to anyone who handles bones of both small and large anomodonts, side by side, is that the smaller and earlier forms, such as *Diaelurodon*, are—even taking into full account the size difference—much more perfectly “finished” in the sense that proportionately less cartilage appears to have remained at the articular ends of the limb bones, than those of large animals such as *D. halli*, and of the giant limb bones figured long ago by Owen. This fact is remarkable, and deserves much further consideration, which lack of adequate material prevents me from doing.

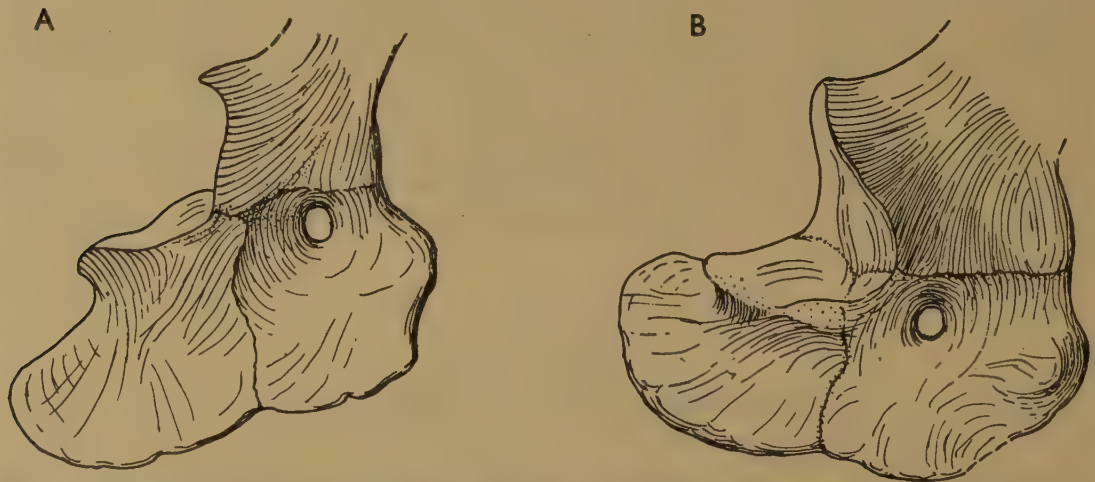


Fig. 20. Dicynodont shoulder girdles of different size drawn the same absolute length, showing how similar they are in general proportions, although one is eight times bigger than the other. Each is a left primary girdle showing the lower end of the scapula articulated to the coracoid and precoracoid.

A, *Diictodontoides skaioi*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P., $\times 2$;
B, an isolated fragment of a giant form from the Cistecephalus zone, Hoek Plas, Murraysburg, C.P., R.498, $\times \frac{1}{4}$.

The general appearance of the limb bones of *Diaelurodon* suggests that its powers of growth were limited, in contrast to the large dicynodonts, even when so enormous as *D. tigriceps*. This matter is one of wide interest because, although individual species of living reptiles have in general a specific size, very rare individuals may live on greatly to exceed it, and it is conceivable that similar events occurred in dicynodonts, as they cannot do in mammals.

Thus, size is a quality not to be used without caution in the determination of reptiles, recent or fossil. Deraniyagala (1939, p. 342) says that *Crocodylus palustris* Kimbala, seen commonly in river mouths in Ceylon, is usually about 300 cm. long, and not infrequently reaches a length of 390 cm.; but it is known to reach a length of 562 cm.

The largest dicynodont skull, *Eocyclops magnus*, from the Cistecephalus zone,

Hout Constant, District Graaff Reinet, now in the South African Museum, measures 79 cm. from the snout to the posterior tip of the squamosal. This skull is commensurate in size with the big shoulder girdle, R.498. The largest skulls available to me, though not comparable with the Cape Town specimen, are the types of *D. leoniceps* and *D. tigriceps* Owen, 43 and 46 cm. respectively in length, though very different in shape. In contrast R.315 is 2.9 cm. long and 1.4 cm. high, and R.237 (the smallest uncrushed specimen) 4.5 cm. long and the same width, though only about 1.7 cm. high.



Fig. 21. Two dicynodont skulls of very different size reduced to the same length for comparison ; both from the Cistecephalus zone.

A, and B, dorsal and lateral views of a skull and lower jaw of R.315, *Oudenodon* sp., Buffels River, O.F.S. $\times 1\frac{1}{4}$. The specimen is a little laterally compressed, but well preserved; it bears a strong resemblance to *D. pygmaeus*, of which a young individual forms Fig. 9, but comes from a different locality and horizon, suggesting that the resemblances depend on some correspondence in size, and perhaps in individual age ; it is the smallest dicynodont skull known to me ; C, the skull of *D. leoniceps*, Owen's type specimen, B.M.N.H. 47047, the largest available in England, $\times \frac{1}{12}$ th approx.

The differences in general proportions between B and C, are shown by the small size of the orbit in the large individual ; the extreme depth of the maxilla below the orbit, and the long snout associated with this great depth. The great depth from the tip of the squamosal to the quadrate condyle in the large skull, and the short comparative distance in the small one, are interesting for they suggest that the mouth could be opened relatively further in the large than in the small individual.

The differences in proportions associated with these size variations are well shown by Fig. 21. In the large animal *D. leoniceps* the orbit is proportionately much smaller, and the supratemporal fossa is correspondingly larger, also the nose is longer, and the depth of the face greater: but the general pattern remains the same.

In order to test the truth of the apparent fact that dicynodonts varied little in shape with variation in size, I have shown drawings of a series of anomodont humeri reduced to the same absolute length (Fig. 22) and arranged in order of size. The smallest measures 11.5 mm., the largest approximately 250 mm., the drawings (all of which are comparable in the sense that the widened distal end lies parallel to the plane of the paper) thus cover a very great range in size. The first is the smallest known humerus, viewed from its upper surface, the last may

belong to the type skull of *D. leoniceps*. It seems evident that the smallest form (probably infantile) is proportionately more slender than the others. *D. pygmaeus* (juvenile) is also slender, but its distal end is not much narrower proportionately than in much larger individuals; it is remarkable, however, for the very distal position of its entepicondylar foramen, and the slenderness of its proximal end.

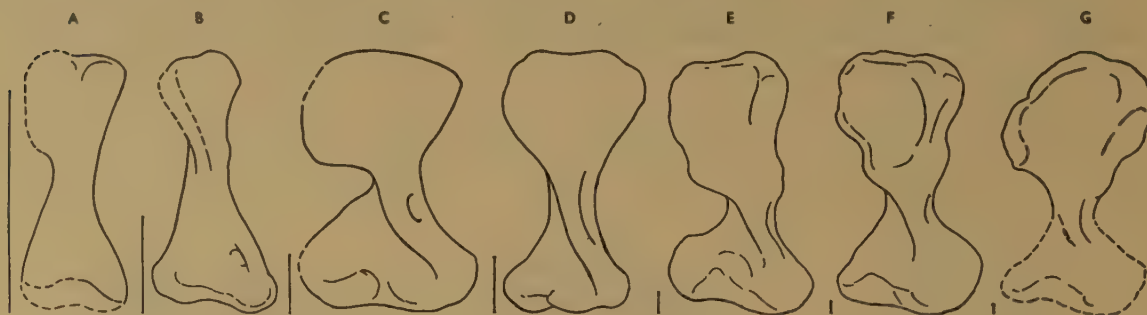


Fig. 22. Dicynodont humeri of the right side, viewed from the lower surface (except for that at the extreme left), and reduced to the same length, to facilitate comparison of shape changes associated with variation in size. The vertical line to the left of each represents one centimetre.

A, *Oudenodon* sp., R.315, ? Cistecephalus zone, Buffels River, O.F.S., infantile; B, *Dicynodon pygmaeus*, R. 443, Lower Endothiodon zone, Hans Rivier Dam, Beaufort West, C.P., juvenile; C, *Dicynodon* sp., B.M.N.H. R.3747, "Near Nieuveltdt"; D, *Diictodontoides skaïos*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P.; E, *Dicynodon halli*, B.M.N.H. R.4067, Upper Endothiodon zone (or Lower Cistecephalus), Kuilspoort, Beaufort West, C.P.; F, *Dicynodon* sp., R.280, Cistecephalus zone, Thabanchu, O.F.S.; G, *Dicynodon leoniceps*? B.M.N.H. 47049.

The other members of the series do not differ from one another consistently in shape with increase in size. Indeed the differences in detail are of such a character as to make it evident that, despite their apparent uniformity, anomodonts do in fact exhibit very considerable variation.

Thus, it is clear that young bones are recognisable from all those of older individuals, and that the variation in shape amongst the latter is much more considerable than would have been expected from a more cursory inspection of the materials. So much so, in fact, that it may imply considerable differences in customary pose, and in the range of movement of the fore limb, amongst the members of the group, and that these differences are not directly correlated with actual size. How far these variations in the shape of the humerus are paralleled by variations amongst other limb bones is unknown, and its significance not entirely clear. The young specimens are intelligible as such: I see no reason why one or other of them could not have grown into any of the large specimens. But the large bones do really differ. It is not evident what alterations in general body shape and in the pose of the limb are associated with the differences between the humeri, and until we get complete skeletons of a good many dicynodonts, large as well as small, it will be impossible to determine the variations within the group.

CONCLUSIONS

The material here described contributes very largely to the basis on which our knowledge of the anomodont skeleton rests. It adds three restorations, each made from a single individual skeleton, to those few which already exist (Fig. 23).

Of the three skulls that of *Diaelurodon*, primitive in retaining teeth in the maxilla in addition to tusks, is long and low. In *Diictodon*, where there is a large tusk, the maxillary process is more marked, the face is deeper and shorter, and the nostril more dorsal. *Diictodontoides* carries these changes even further, the nostril being displaced much dorsally and the maxilla greatly deepened below it.

Diaelurodon appears to have been in all probability a more active animal than either of the others, its limb bones are better "finished," and their cartilaginous caps smaller. Its vertebral column is remarkable because the neural spines throughout (except for the axis and third cervical vertebra) are all very similar, short but noticeably erect. They show the normal condition of having two-headed ribs back to the eighth vertebra, followed by single-headed ribs which extend to the pelvis. In contrast, in *Diictodon*, although the transition from two-headed to single-headed ribs occurs at about the same place, the vertebral column is a good deal diversified because from the fifth vertebra the neural spines, though short, slope progressively more and more backward until very suddenly at the tenth or eleventh vertebra they become upright again. *Diictodontoides* much resembles *Diictodon*, though all the vertebrae are noticeably heavier in build, the centra being relatively much larger than in the other two, although the animal is only about half as large again. The slope of the neural spines in *Diictodon* and *Diictodontoides* presumably implies increased flexibility in the back with consequential modifications in locomotion.

It seems clear that the neck passed into the body so gradually that it is impossible to determine where the thoracic series of vertebrae actually begins, but it is somewhere near the seventh vertebra. The character of the neck, with its ribs relatively short, but none the less hardly shorter than the first thoracic, implies that the shoulder girdle, unlike that of mammals, is not supported posteriorly by serratus muscles rising from pectoral ribs firmly anchored at both ends, but is attached largely by the clavicular and inter-clavicular connections to the sternum, the serratus muscles of the scapula presumably being relatively small, and nothing being known of those which pass to the head, though they may well have been considerable.

The fore limbs of *Diaelurodon* and *Diictodon* have a real resemblance; the humeri conform to the same pattern, although curiously enough the coracoidal part of the shoulder girdle differs considerably between the two forms. In *Diaelurodon* the fore arm has an ulna with an olecranon process, and a very mammal-like elbow. The corresponding joint of *Diictodontoides* retains a great deal of cartilage and is less well "finished," more clumsy in appearance. Furthermore in *Diictodontoides* the fingers radiate outwards so as to form a very wide, paddle-like hand, presumably well adapted for swimming.

The pelves of the three animals differ considerably in ways which it is singularly

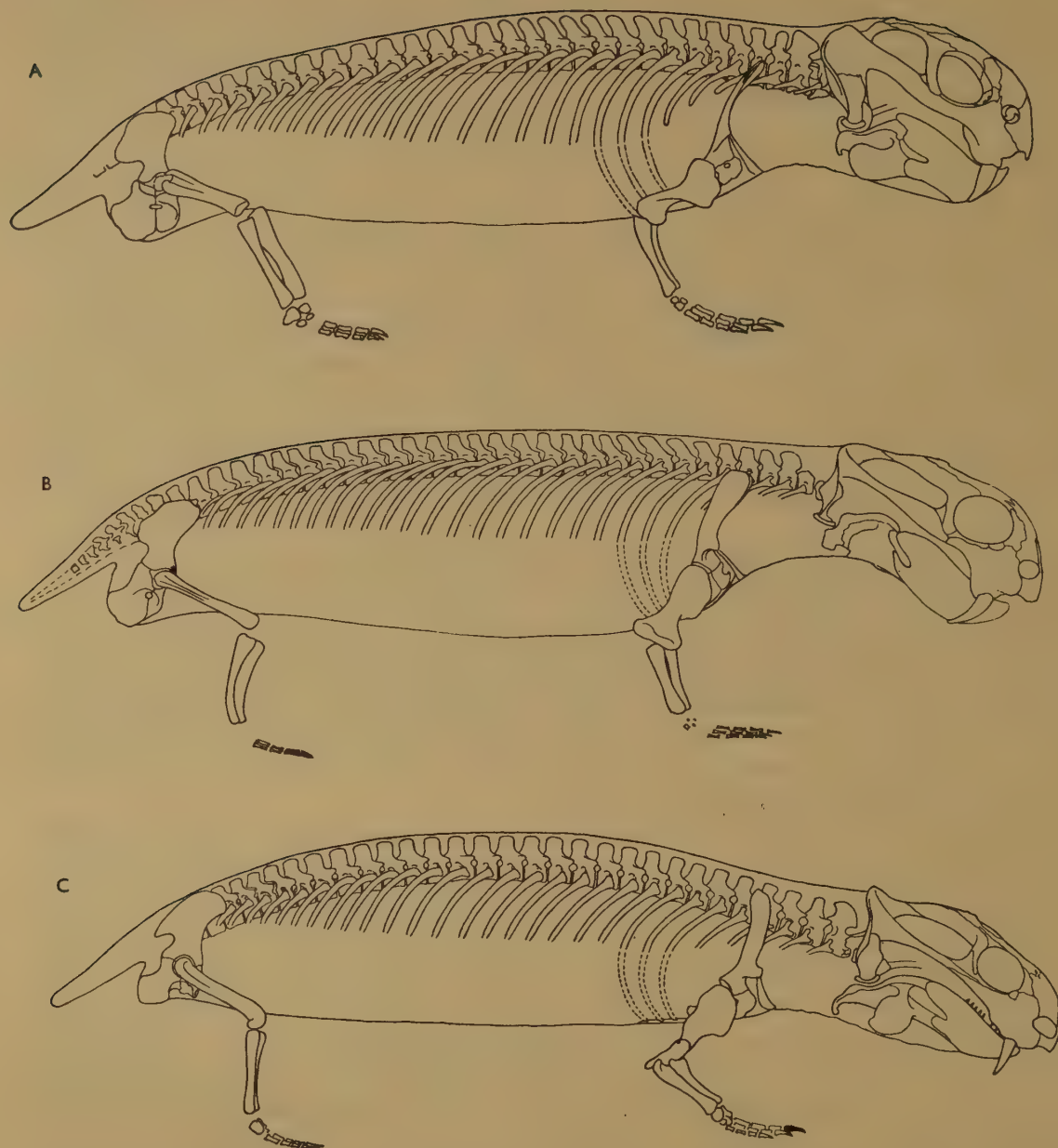


Fig. 23. Restorations of the skeleton of three anomodonts, each made from a single individual. A, *Diictodontoides skaios*, gen. et sp. nov., R.396, Cistecephalus zone, Murraysburg, C.P., B, *Diictodon sesoma*, sp. nov., R.314, ? Cistecephalus zone, Buffels River, O.F.S., C, *Dialeurodon whaitsi*, Broom, R.451, Lower Endothiodon zone, Beaufort West Commonage, C.P. All approximately $\frac{1}{3}$ rd natural size.

[Continued facing page]

difficult to account for. That of *Diaelurodon* is well finished, and, with a great excavation of its lower surface, seems fitted to give attachment to muscles which will pull the femur forward and backward and enable it to carry the animal's weight. The curiously sloping position of the pelvis in *Diictodon* implies that the muscles which drag the femur forward do not come from the pubis, for the acetabulum has an extremely anterior position. In *Diictodontoides* the pubis is a relatively large bone, and it seems quite clear that the acetabulum faces almost directly outwards. The femur suits this condition because, as in the other limb bones of this animal, it evidently possessed a thick cartilaginous head which articulated with the acetabulum so that its direction was largely outwards. In other words the hind legs of *Diictodontoides* are not at all "mammalian" in character, for they are relatively short and belong to a rather clumsy animal, not fast moving on land, but capable of swimming effectively, like a sea lion.

Diaelurodon has a foot with very long claws much of the monotreme pattern, perfectly adapted for digging, whilst the foot of *Diictodontoides* has thick, clumsy phalanges, the short terminal ones suggesting that the claws were short, more so, even, than those of the hand.

However, from a consideration of the three specimens it appears that very little change takes place in the general build and structure between *Diaelurodon*, the earliest form, and the later dicynodonts. All of them are long-bodied animals apparently with a short tail, which appears to have been mammal-like in that it arises from the blunt hinder end of the body as a small process continuing the vertebral column; the condition is, in fact, mammal-like in a way not paralleled by any other adequately known group of reptiles. Even in scattered specimens of dicynodont vertebrae caudals are exceedingly rare; if the tail had been long, one would have expected to find a sample of them, so that their rare occurrence seems to confirm the suggestion that the tail was short, and not heavy. How

The only authentic vertebral column is that of *Diaelurodon*, the others, though represented by long continuous stretches of vertebrae, are incomplete and have been given arbitrarily the same number of vertebrae; ribs in effect are conventional, though their articular ends are genuine, and the general distribution is substantiated; the placing of the shoulder girdle in *Diaelurodon* depends on its position in the specimen with relation to the skull, in the other two forms the specimens give no guide so the girdle is placed by analogy with *Diaelurodon* and with R.443 (Fig. 9); the full number of digits is not shown because the hands and feet are seen directly from the side; the only tail about which there is direct evidence is that of *Diictodon*, where the five caudal vertebrae figured are present, the other tails are restored by analogy with it; the tail is shown as of a mammalian type, that is, a small appendage rather than a conical end to the body, the evidence is necessarily fragmentary but depends on a judgment of the last visible caudal vertebra in *Diictodon*, which is on the level of the hinder border of the ischium, and has a strong transverse process, agreeing in all general characters with the caudals visible in front of it; the general implication is that the tail is narrowing rather rapidly and that it was mobile and muscular. It is evident from this figure that the three individuals show a progressive deepening of the skull as a whole, and especially of the premaxilla below the nostril. This is interesting because it suggests that the extreme height of the nostril in the aquatic *Lystrosaurus* represents a logical end to the series of changes shown in these three earlier forms.

far this bears on the attribution of those tracks which it is natural to believe were made by dicynodonts, one of which shows a tail streak, is uncertain.

One feature in which mammal-like reptiles as a whole contrast with sauropsid reptiles is that in them the tail tends to be short. Complete tails are unfortunately scarcely known, though a specimen of *Lystrosaurus* (Watson 1911) shows a virtually complete short tail of ten vertebrae, but such evidence as we have suggests that dicynodonts, and indeed all anomodonts, had a conical tail with a dozen or so vertebrae. Only one group, the Dromasauria, as Broom pointed out in his first description of them, are provided with an immensely long tail, but it is flexible and capable of being wrapped round the whole body, as for example in a squirrel, and is quite unlike the long tail of such a lizard as *Varanus*. This curious fact suggests that the dicynodont tail shortened and effectively vanished because it would play no serious part in the animal's activity; the dromosaur tail was probably functional, though in what way we do not know.

The stride of *Dicynodon*, although short because the limb bones are short, was clearly very much bigger than in pelycosaurs, and the gait was not straddling as in them. The feet of opposite sides, though they are considerably separated, are not parted to the extreme extent found in Lower Permian reptiles.

These limbs, with their powerful muscles, could evidently raise the body above the ground and enable it by more precise movement to walk more quickly than such earlier forms as the pelycosaurs. Types of track, known by my specimen from the Karroo, and others from Upper Permian rocks in Europe, seem such as would have been made by dicynodonts. These tracks show that although the feet of opposite sides were well separated, so that in general probably one foot moved at a time and the body swung from side to side, the stride was relatively long, and the animal evidently capable of effective walking.

The elongated body and relatively short limbs of *Dicynodon* presumably imply, and depend upon, the provision of a very large abdomen to contain a gut sufficient in volume to hold large meals of plant, and to allow of their probably rather protracted digestion. The rate at which digestion proceeds within the body of an animal depends, amongst other things, on the temperature at which it takes place. Mammals and birds by their high and constant body temperature are enabled to digest their food more quickly than can any reptile, whose body temperature varies with that of its surroundings. This is exceedingly obvious in, for example, the case of a snake where a meal, usually of one complete animal, may need a period of weeks for digestion.

In dealing with *Dicynodon* it must always be remembered that it is a reptile, and it is therefore natural to conclude that it does not possess the high body temperature whose maintenance in a mammal employs a proportion of the energy available in the food. Casual observations made in a country like the Karroo, in which tortoises are common, suggest that they spend only a relatively small part of the day feeding, so that *Dicynodon's* food requirements may well have been relatively small compared with its weight, enabling it to dispense with any equivalent of the grazing habits of ungulates, and may have allowed it to eat all it needed, even in a country of sparse vegetation, in comparatively short feeding periods.

That the general build of my three anomodonts appears more slender than would have been expected is probably a mere size effect; it contrasts vividly with Helga Pearson's drawing of the huge *Kannemeyeria*, which agrees in the main with the skeletons of other large dicynodonts from Brazil and East Africa.

The extreme abundance of dicynodonts in the Permian part of the Karroo, and in East Africa, is most striking. Only in the Cutties Hillock Sandstones of Elgin, Scotland, does a parallel exist. The later dicynodonts are all large (sometimes very large) animals, and it may be supposed that their food differed to some extent from that of the small dicynodonts which, to the end of the *Cistecephalus* zone, formed so large a part of the population of the Karroo plains.

This is a matter of great general interest: we have in the anomodonts the first group of herbivorous vertebrates in a fauna to have become dominant over other tetrapods, which were carnivores. In fact they are the fore-runners of the abundant vegetarian land forms, culminating in the great herds of ungulates, and the innumerable rodents, which have characterised mammal faunas from Eocene times until today.

The dicynodonts of the *Cistecephalus* zone effectively die out at the end of that time. *Lystrorhynchus*, an aquatic modification, lives on, enormously abundant, in South Africa, in China and in India. After this animal had gone there are giant dicynodonts in many places—North and South America, East Africa, eastern Asia, India and Europe—but they no longer form a group varied in size and in bodily shape, fitted to eat plants of all kinds, and to provide a food supply for the maintenance of a varied population of carnivores.

These survivors pose many problems. Why should the overwhelming majority of dicynodonts, and their predators, suddenly die out? And why should the giant members survive? The contemporary lines leading to mammals consist of small, or very small creatures, not competing with dicynodonts at all: indeed they are probably insectivorous, and hence in competition largely with non-mammal-like reptiles. The fact that the herbivorous tritylodonts, a small and rather uniform group, lived on from the Trias into the Lower Jurassic suggests that only in still later times did mammalian predominance become so effective as to cause their extinction.

What did the few surviving dicynodonts eat? And what animals ate the land flora which succeeded that of the Upper Permian of the southern hemisphere. Is, in fact, the thinning of the dicynodont population really a measure of the disappearance of the plant *Glossopteris* and its associates?

This possibility deserves examination; the flora of the *Cynognathus* zone of South Africa is partly known, and does not possess *Glossopteris*, and it seems that—despite earlier statements—*Glossopteris* has not, in fact been found in Russia, so that there is evidently no necessary association of the animal and the plant.

None the less, the fact that those dicynodonts which survive into the Trias are in general large animals—no parallel to the abundant fauna of small animals of that group found throughout its range in Permian times—is very remarkable, for so far as it is known the fauna of the *Cynognathus* beds, and of all the rocks of the same age throughout the world, is completely lacking in any herbivorous

tetrapod of medium or small size. The economy of the fauna and flora of later Triassic times is entirely obscure, and nothing is known of land living herbivorous reptiles, except for the large Rhynchocephalia, and the tortoises in extreme Upper Triassic rocks.

Thus, we are presented with an apparent parallel to the conditions existing in Upper Devonian and Carboniferous times, where all the known amphibia, large and small alike, seem singularly unfitted to eat plants of any kind, and must have lived on animals, as the small rhachitomous *Eugyrinus* is known to have eaten insects.

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EXPLANATION OF THE ABBREVIATIONS USED IN THE TEXT FIGURES

Ac.	acromium	Lac.	lachrymal
Acet.	acetabulum	M.C.1	metacarpal 1
Ang.	angular	M.T.5	metatarsal 5
Ant.	maxillary antrum	Mx.	maxilla
Ant.Zyg.	anterior zygapophysis	N.C.	neural canal
Art.	articular	N.Sp.	neural spine
Art.Fac.	articular facet, possibly for clavicle	N.Sp.At.	neural spine of atlas
C.H.	caput humeralis	Na.	nasal
Cap.	capitulum of rib	Not.	notochord
Caud. 1, 2, 3,	caudal vertebrae 1, 2, 3	Not.For.	notochordal foramen in odontoid
Caud.Rib.	caudal rib	Obt.For.	obturator foramen
Cent.	centrale (navicular)	Oc.Con.	occipital condyle
Clav.	clavicle	Odon.	odontoid process (centrum of atlas)
Clei.	cleithrum	P.Mx.	premaxilla
Cor.	coracoid	P.O.	postorbital
D.C. 1	distal carpal 1	P.Par.	preparietal
D.Tar. 1	distal tarsal 1	Pal.	palatine
Dent.	dentary	Par.	parietal
Dep.Mx.	depression in maxilla	Par.Oc.	paroccipital
E.S.P.Mx.	eroded surface of premaxilla	Par.Oc.Proc.	paroccipital process
Ect.	ectopterygoid	Pin.For.	pineal foramen
Ent.For.	entepicondylar foramen	Post.Zyg.	posterior zygapophysis
Ex.Oc.	exoccipital	Post.Zyg.26	posterior zygapophysis of ver- tebra no. 26 in section
Fac.	facet on distal tarsal 3 which articulates with distal tarsal 5.	Pr.Cor.	precoracoid
Fac.I.Cen.	facet for articulation of first intercentrum	Pr.Cor.For.	precoracoid foramen
Fac.R.	face on the ulna for articulation of the radius	Pr.Fr.	prefrontal
Fb.	fibulare (calcaneum)	Pr.At.	proatlas
Fen.Ov.	fenestra ovalis	Pt.	pterygoid
Fib.	fibula	Pt.Fr.	postfrontal
Fl.P.Mx.	median septum made by the premaxilla	?Pt.Fr.	?postfrontal
For.Mag.	foramen magnum	Pub.	pubis
Fr.	frontal	Qu.	quadrate
Glen.	glenoid cavity	Qu.J.	quadratojugal
Gr.Sp.C.	floor of the canal for the spinal cord	R.Art.Proc.	retroarticular process
Hum.	humerus	R.Fac.	facet on humerus for the radius
I.C.	intercentrum of atlas	Rad.	radius
I.C.1	intercentrum 1	Rd.	radiale
I.Cl.	interclavicle	Ref.Lam.	reflected lamina
I.Par.	interparietal	S.Ang.	surangular
Il.	ilium	S.Mx.	septomaxilla
Int.	intermedium	S.Oc.	supraoccipital
Int.Nar.	internal nares	Sac.1	sacral vertebra 1
Isc.	ischium	Sac.R.1,2,4	first, second and fourth sacral ribs
Ju.	jugal	Scap.	scapula
L.J.	lower jaw	Sp.	splénial
		Sp.N.1	first spinal nerve
		Spin.Can.	spinal canal
		Sq.	squamosal
		St.	stapes

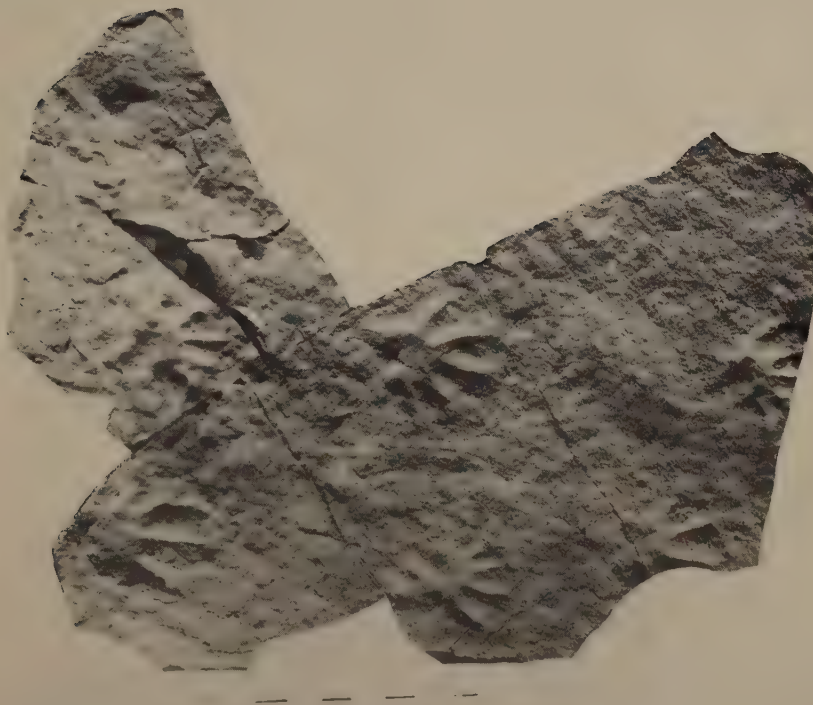
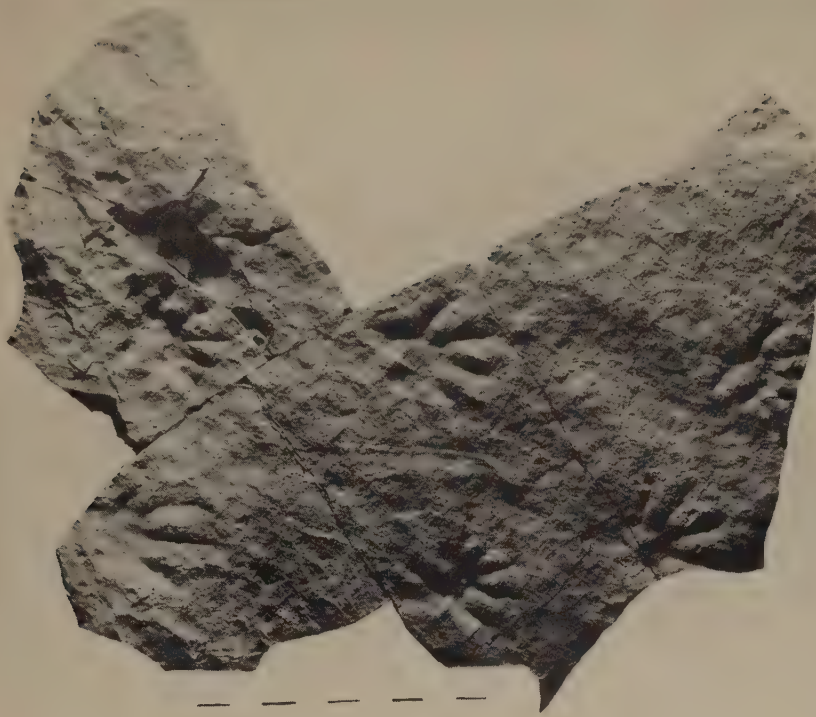
St.Rib.1	first sternal rib	Tusk	canine tusk
Stern.	sternum	U.Fac.	facet on humerus for the ulna
Tab.	tabular	Ul.	ulna
Tb.	tibiale	Un.	ulnare
Tib.	tibia	Vert.Cent.	vertebral centrum
Tr.Proc.	transverse process	Vert.Col.	vertebral column
Trans. Proc.	transverse process of atlas	Vert.6	sixth vertebra
Troc.	trochanter	Vo.	vomer
Tub.	tuberculum of rib		

PLATE 1

The anomodont skeleton.

Two photographs of the same footprint slab, lighted from opposite directions. Just under half size.

The specimen, R.321, was found at Middelburg, Cape Province, in a very fine-grained sandstone which breaks with an almost conchoidal fracture, and is probably from the base of the *Lystrosaurus* zone. It shows six prints of the track of a reptile, clearly an anomodont. Fore and hind prints alternate, and the stride is very considerable. The track is in no way sprawling, but is not that of a very active animal, for the distance between a fore foot impression, and that of the hind foot which lies alongside, is about the same as the width of a hand, and about a fifth of the stride. The large prints are clearly hands, the smaller feet : in each case in addition to the impression of the digits there is a considerable palm, or sole imprint behind them. The fingers, or toes, make an almost V-shaped impression, the spaces between them forming rather rounded ridges. Between the imprints of a fore and hind foot at one point, over a distance of some 3 cm., there is the evident impression of a tail. It consists of a rather narrow groove with a curious central raised ridge, a condition not very easy to explain but clearly dependent on the physical condition of a sand/water mixture.



The anomodont skeleton.
Two photographs of the same footprint slab, lighted from opposite directions (just under half size).

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**Scientific results of an inquiry into the ecology and economic status
of the Nile Crocodile (*Crocodilus niloticus*) in Uganda and
Northern Rhodesia**

By

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High Commission; and the Government of Northern Rhodesia*

SYNOPSIS

During the past decade the Nile Crocodile has been greatly reduced in numbers. Scientific information on the general and breeding biology was deficient and research urgently required to ascertain the possible effects on fisheries of further drastic reduction by commercial exploitation. The results reported are based upon observations made in Uganda, Northern Rhodesia, Barotseland and Zululand during 1952, 1956 and 1957.

The diurnal rhythm of activity is related to feeding and thermal requirements. Thermoregulation, at about 25.5° C., is effected by habitat selection and behavioural adaptation. Information is given on terrestrial and aquatic locomotion, respiration and diving times. Evidence is presented that stomach stones, always present in the adult, are deliberately swallowed and subserve hydrostatic functions. Rate of growth is most rapid, about 265 mm. per annum, in early life : it decreases progressively to about 35 mm. per annum or less. The sexes are equal in numbers : the males grow more rapidly and attain larger size than the females.

Sexual maturity is attained at a length of about 2.9 to 3.3 metres in the male, and about 2.4 to 2.8 metres in the female, and at an estimated age of not less than nineteen years. The breeding season, which differs with locality, coincides with the period of low water levels. Aspects of breeding behaviour in the male, including territorial defence, combat and vocalization are discussed. A pre-nuptial display in the female and initial stages of copulation have been observed. An account is given of colonial nesting grounds, nest sites, clutch sizes and parental care by the female. Juveniles are ecologically separated from the adults.

A detailed survey is made of the food and feeding habits : the diet is extremely varied ; it changes progressively with the crocodile's age ; and differs according to locality. Data relating to predatory enemies, parasites and injuries, and an account of commensal relations with three species of birds, are given. Attention is drawn to the complex web of relationships in which the species plays a part as master predator, cannibal and scavenger : its status in relation to man and to commercial fisheries is reassessed. It is concluded that *C. niloticus* is a valuable member of the African fauna ; and recommendations are made for its conservation.

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INTRODUCTION

The trade in crocodile leather has in recent years grown to the proportions of almost a major industry in various East and Central African territories, from which thousands of skins are exported each month. As a result of this commercial exploitation, the Nile crocodile is being rapidly reduced and in some localities its continued existence is threatened.

Meanwhile surprisingly little scientific information has been published on its general biology and economic status. Further research was clearly needed in order to assess the probable effect which extermination or drastic reduction of crocodiles may have in the economy of inland waters and in particular on commercial fisheries.

At the invitation of the Government of Northern Rhodesia, and with this problem in view, a survey was undertaken in 1956 in the swamps of Bangweulu and Mweru Wa Ntipa in the Northern Province. The following year the investigation was continued in the riverine habitats of the Luangwa, Kafue and Upper Zambesi valleys in the Central and Southern Provinces, and Barotseland. Previous work had already been carried out in Uganda in 1952, and was continued during subsequent visits to Uganda, and in Zululand.

LOCALITIES AND MATERIAL

The results to be discussed in the following pages rest upon two types of information, namely : that derived from observation of free-living crocodiles ; and that from the examination of freshly-killed material.

Observations on crocodiles in the natural state were mostly made along the eighteen-mile reach of the Victoria Nile from Murchison Falls to the Lake Albert delta. These waters support a concentration of crocodiles which, in number and size, is probably unrivalled today anywhere in Africa. The area thus provided an ideal base for ecological studies and photography. The work was carried out during four visits: in July and December, 1952 ; June to August, 1956 ; and December to January, 1957. Camps and nearby observation posts were established at various points below the Falls and above Magungu in specially favoured localities where large concentrations of the reptiles were available for undisturbed, close-range study from hides. Further observations were made in the Hluhluwe, Umfolozi, Ndumu and St. Lucia Game Reserves of Zululand. A detailed photographic record was obtained. Some of the results (of which only a few appear here) showing crocodiles in their pristine state, are of special interest because—as a result of hunting, poaching and general disturbance—the scenes they depict are rapidly disappearing.

These studies were supplemented by the examination of a large series of specimens in Uganda, Rhodesia and Barotseland. A standard routine was developed for the examination of material—it being necessary to systematize procedure since in the heat of the tropics crocodiles had to be skinned with the least possible delay. Each specimen of the night's catch was first toe-marked, and a serial

number assigned to it. All data were set down on printed Record Sheets, one for each crocodile examined. Prior to skinning, about forty measurements of various parts of the body were taken with steel-tape and calipers. (Such measurements were required for studies of relative growth and—apart from the key-measurement of total length from snout to tail-tip—will not be considered in the present paper). Other information recorded at this stage included notes on external characters, scute- and tooth-counts, abnormalities, injuries, the location and density of leeches ; and specimens small enough were weighed entire on a spring-balance or yard-arm. In the case of large crocodiles the skin was weighed separately and the carcass dismembered and weighed in parts. After the skinners had completed their task, the stomach was removed, opened in a basin, and flushed with water prior to examination of its contents. The weight of stomach stones was recorded ; and the sex and state of the reproductive organs and the presence of parasites noted. A complete examination of every crocodile was not always possible : in particular, information on internal parasites and on the condition of the gonads is often wanting. On the other hand, in all cases full information was recorded for stomach contents ; and the above-mentioned pre-skinning routine was nearly always carried out in full.

Five hundred and seventy-six crocodiles were examined by the writer in the course of the investigation. Serial numbers, with dates and localities for this material, are listed below. The information thus obtained, together with some additional records on stomach stones and prey organisms received from other sources (see pp. 236, 278) is set out and discussed in the relevant sections of the report.

UGANDA

Lake Victoria :	Sese Is. : 2 (16 Jan.), 101 (10 Nov. 1952).
	Damba Channel : 70-73 (2-4 Sept. 1952).
	Bukafu Bay : 64-67 (28-29 Aug. 1952).
	Nsadsi : 68 (1 Sept. 1952).
	Bulago : 69 (2 Sept. 1952).
	Buka Bay : 75-79 (4 Sept. 1952).
	Masovwe : 74, 80 (4-5 Sept. 1952).
	Buvu : 100 (9 Nov. 1952).
	Buluba Bay : 43-63 (22-25 Aug. 1952).
	Napoleon Gulf : 1 (9 Jan.), 8 (27 Mar.), 9 (2 April), 11 (8 April), 42 (22 Aug.), 82-94 (6-8 Oct.), 103 (7 Dec. 1952).
	Kigi Is. : 4-7 (4-7 Mar. 1952).
	Jinja : 3 (5 Feb.), 27 (8 July), 38-41 (7-22 Aug.), 81 (12 Sept. 1952).
	Namasagale : 10 (5 April), 95-99 (29-30 Oct. 1952).
Victoria Nile :	Fajao : 32-37 (21-24 July 1952).
	Magungu : 28-31 (17-19 July 1952), 106-109 (1-6 Aug.), 222 (29 Dec. 1956), 223 (2 Jan. 1957).
Lake Albert :	Butiaba : 102 (22 Nov.), 104, 105 (17 Dec. 1952).
	Kaiso : 20-26 (22-23 June, 1952).
	Ntoroko : 14-19 (15-21 June 1952).
Semliki River :	Bweramule : 12, 13 (15-23 April 1952).

NORTHERN RHODESIA

- Bangweulu Swamp : L. Kinweshewa : 110 (17 Aug. 1956).
 Panta Point to Chilubi : 111–115 (19 Aug.), 157 (6 Sept. 1956).
 Lake Chali : 116–119 (21 Aug.), 156 (30 Aug. 1956).
 Kansenga : 120 (21 Aug. 1956).
 Miloki : 121–123 (22 Aug. 1956).
 Bwalya Mponde : 124–135 (23–25 Aug. 1956).
 Mutwamina : 136–146 (26 Aug. 1956).
 Matongo : 147–155 (27 Aug. 1956).
 Mweru Wa Ntipa : 158–208 (12–15 Sept. 1956).
 Kalungwishi River : Olandi : 209–220 (18–19 Sept. 1956).
 Luangwa Valley : Lunsemfwa R. west of Rufunsa : 224–243 (2–3 Aug. 1957).

- Lunsemfwa R. east of Rufunsa : 244–257 (4–5 Aug. 1957).
 Musukwe Lagoon : 258 (5 Aug. 1957).
 Lower Lunsemfwa R. : 273–282 (9 Aug. 1957).
 Luangwa R., Beit Bridge : 259–272 (7 Aug. 1957).
 Luangwa R., Nytande : 283–301 (11 Aug. 1957).
 Luangwa R., Ndevu : 302–320 (13–14 Aug. 1957).
 Kafue Flats : Chembe : 321–322 (22 Aug. 1957).
 Nampongwe R. : 323–336 (23 Aug. 1957).
 Luwato R. : 337–339 (24 Aug. 1957).
 Lochinvar Swamp : 340–363 (25 Aug. 1957).
 Chimwajila : 364–373 (26 Aug. 1957).
 Iyeshya : 374–412 (29 Aug. to 1 Sept. 1957).

BAROTSELAND

- Upper Zambesi : Mongu to Lukulu : 413–428 (10 Sept.), 437–448 (12 Sept.), 481–499 (15 Sept. 1957).
 Mongu to Senanga : 429–436 (11 Sept.), 449–480 (13–14 Sept.), 500–576 (16–20 Sept. 1957).

ZULULAND

- St. Lucia : 221 (24 Oct. 1956).

*PART I. GENERAL BIOLOGY**DIURNAL ACTIVITY RHYTHM*

The diurnal movements of the Nile Crocodile have been remarked upon since ancient times. Thus, Pliny (Holland, 1601) observed : “All the day time the Crocodile keepeth the land, but he passeth the night in the water.” But information of a more than anecdotal character on behaviour in relation to the diurnal cycle is extremely scanty. The observations here described are of two kinds—general, and counts made from observation posts.

General observations

Numerous observations made at different hours of the day and night, along the Murchison reach of the Nile between Fajao and Magungu, in the Lower Semliki, and Lakes Albert, Kioga and Victoria, provide a general picture of the activity

rhythm in tropical waters. The combined data, for crocodiles lying (i) on land, (ii) with part of the body in the water, and (iii) in water, are given in Table 1, and expressed graphically in Fig. 1.

The crocodile is nocturnally aquatic. Movement to the water has already begun before sunset, and during the hours of darkness virtually the whole population is afloat. My Uganda records for the hours between midnight and dawn are few ; but the results are fully confirmed from Northern Rhodesian specimens—almost

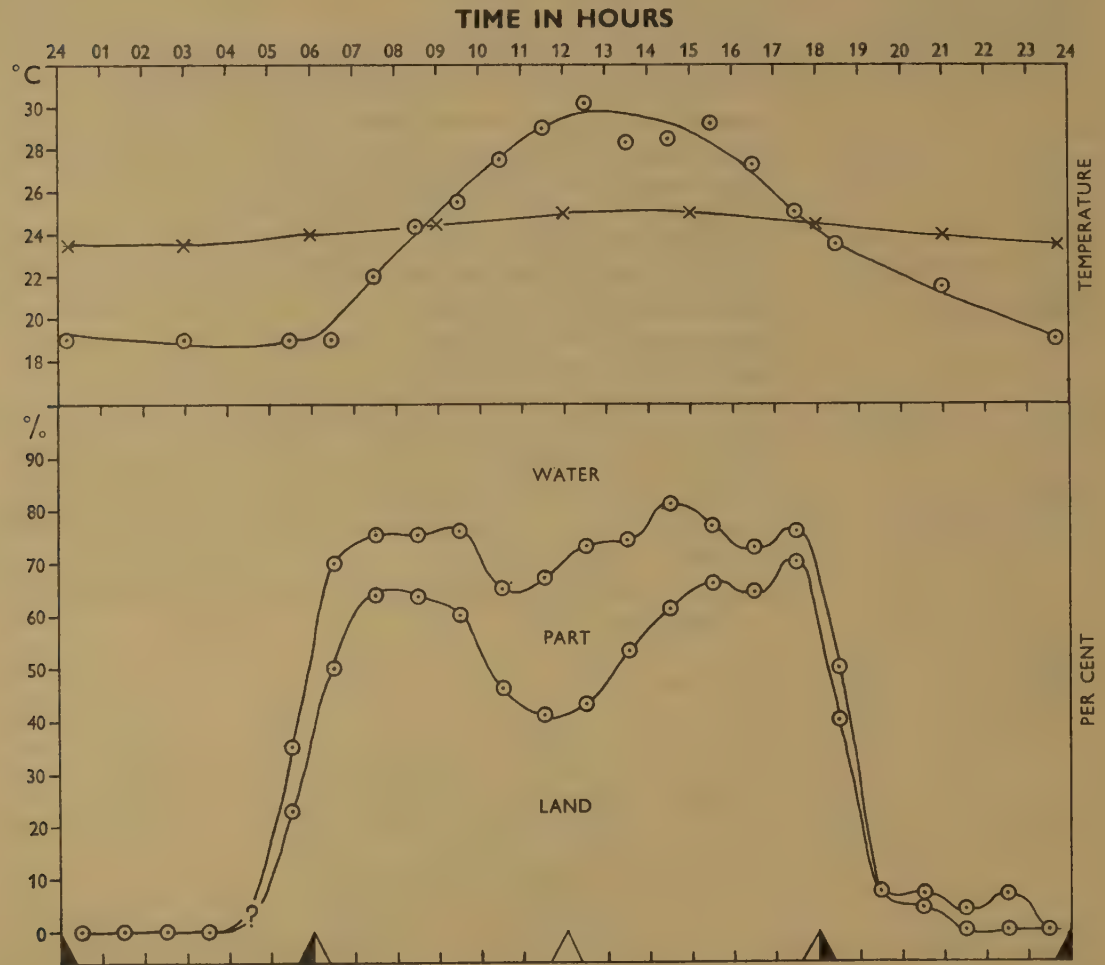


Fig. 1. Diurnal activity rhythm : showing, for hourly periods, the percentage of crocodiles counted ashore, partly in the water, and in the water. Mean shade and water temperatures are shown above.

all of which were shot in the water at night. Mr. H. Holloway, who has hundreds of night-long hunts to his credit, tells me that in his experience perhaps one in thirty crocodiles may be seen lying out on grass or papyrus at night, though the tendency to come ashore is more noticeable in rough weather (see p. 233).

The general movement from water to land begins in the hour before sunrise : thereafter the egress is rapid and by about 0730 hrs. (sun time) three-quarters of the population will have hauled out. There are two main basking periods—in

TABLE 1

Number of crocodiles counted lying ashore, partly in the water, and in the water, by hourly periods.

<i>Time</i>	<i>Land</i>		<i>Part</i>		<i>Water</i>	
	<i>No.</i>	<i>Percentage</i>	<i>No.</i>	<i>Percentage</i>	<i>No.</i>	<i>Percentage</i>
2400-0100	0	0.0	0	0.0	6	100.0
0100-0200	0	0.0	0	0.0	7	100.0
0200-0300	0	0.0	0	0.0	3	100.0
0300-0400	0	0.0	0	0.0	3	100.0
0400-0500	—	—	—	—	—	—
0500-0600	6	23.1	3	11.5	17	65.4
0600-0700	129	50.4	50	19.5	77	30.1
0700-0800	631	63.7	116	11.7	244	24.6
0800-0900	750	63.8	139	11.8	286	24.3
0900-1000	649	60.4	170	15.8	256	23.8
1000-1100	405	46.2	167	19.0	305	34.8
1100-1200	349	41.5	213	25.4	278	33.1
1200-1300	438	43.1	307	30.2	272	26.7
1300-1400	558	53.5	215	20.6	270	25.9
1400-1500	792	61.1	259	20.0	245	18.9
1500-1600	597	66.3	94	10.4	210	23.3
1600-1700	519	64.6	64	8.0	220	27.4
1700-1800	29	70.7	2	4.9	10	24.4
1800-1900	3	30.0	1	10.0	6	60.0
1900-2000	2	7.7	0	0.0	24	92.3
2000-2100	2	4.7	1	2.3	40	93.0
2100-2200	0	0.0	2	4.2	46	95.8
2200-2300	0	0.0	2	7.4	25	92.6
2300-2400	0	0.0	0	0.0	13	100.0

the morning between 0700 and 0930 hrs., and in the afternoon between 1430 and 1730 hrs. In the heat of the day when the sun is high and shadows are short, there is a secondary movement back to the water, and by midday only about 40 per cent. of individuals are seen ashore. After the second basking period there is a rapid return to the water: this movement begins about half an hour before sunset, and as darkness falls the grounds are once again deserted.

Observation posts and crocodile counts

To obtain more precise information on activity during the daylight hours, in relation to environmental factors, observation posts were established at two selected sites where crocodiles were both plentiful and relatively free from disturbance. Their location is shown in a sketch map (Fig. 2) largely based upon air photographs supplied by the Directorate of Overseas Surveys.

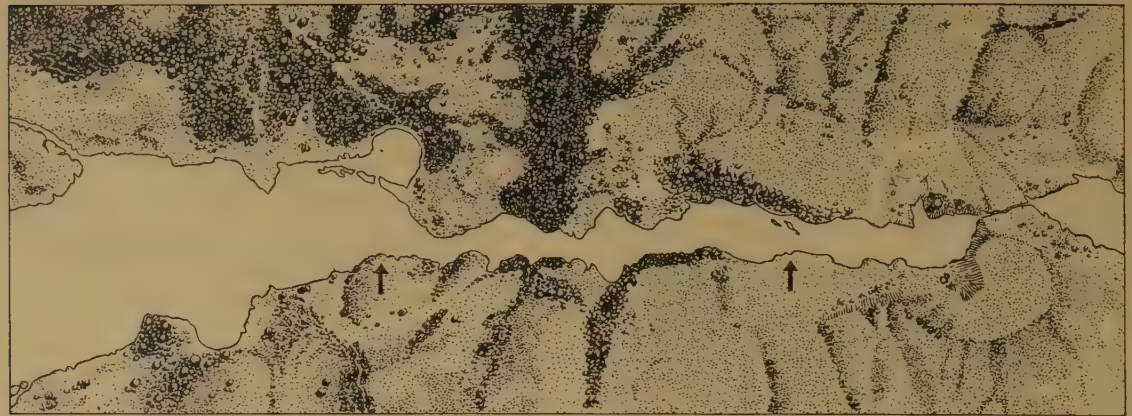


Fig. 2. Sketch map of the Victorial Nile below Murchison Falls. The arrows indicate the position of observations posts: left, Fajao O.P.; right, Murchison Falls O.P.

Murchison Falls O.P.

This observation post was situated on the steep south bank of the Nile, overlooking two rock islets about 850 yards below Murchison Falls (Plate 1, fig. 2). The elevated vantage point afforded a clear view not only of crocodiles ashore and awash round the islets and on a sector of the tree-shaded bank opposite, but also, owing to the narrowness of the river (about 120 yards) and clarity of the water, those which were keeping station against the current or lying submerged in shallows. The reptiles were entirely free from human interference, since the place was inaccessible by launch.

Fajao O.P.

The second post was on a hill top east of Fajao jetty, overlooking the Nile where it broadens from the hill-girt gorge into an estuary some 350 yards wide. This station commanded, at rather long range, a broad view of the north bank—embracing several isolated basking places, a large sand-spit, a lagoon, and an important sunning and breeding ground below the escarpment. The site offered a great concentration of crocodiles—the largest number counted *ashore* at one time being 158.

Crocodile counts

At Murchison O.P. counts of crocodiles lying (i) ashore, (ii) partly in and partly out of the water, and (iii) afloat or submerged, were recorded for each 15-minute observation period from 0700 to 1700 hrs. on the 8th, 10th and 12th July, 1956, and 4th Jan. 1957. The general state of the weather and the air temperature (shade) were also recorded for each observation period (see Table 2, and Fig. 3, a to d).

TABLE 2

Data for four ten-hour observation periods at Murchison O.P.; showing the number of crocodiles counted : *L*—lying ashore ; *P*—with part of the body in the water ; and *W*—in the water.

Time	8.7.56				10.7.56				12.7.56				4.1.57			
	Temp.	L.	P.	W.	Temp.	L.	P.	W.	Temp.	L.	P.	W.	Temp.	L.	P.	W.
0705	21.0	12	0	14	22.0	32	4	12	20.0	10	1	25	23.0	5	4	3
0720	—	5	2	14	23.0	31	5	9	21.0	10	4	23	22.5	7	5	5
0735	20.0	5	2	19	24.0	34	6	13	22.0	10	5	19	23.5	6	5	4
0750	—	5	3	22	24.0	31	4	11	22.5	9	2	20	24.0	6	4	7
0805	20.5	6	3	20	25.0	33	2	15	24.0	9	4	11	26.0	6	3	7
0820	—	7	3	25	25.5	27	4	12	25.0	9	6	4	25.5	5	3	6
0835	21.0	8	2	19	26.0	31	5	10	26.5	9	5	12	25.0	5	3	7
0850	—	9	6	23	26.0	30	7	14	27.5	10	8	11	26.0	4	3	11
0905	21.0	9	5	26	27.0	31	5	11	29.0	11	5	22	25.5	2	4	10
0920	—	8	9	18	27.0	32	6	12	29.5	9	2	7	27.5	2	5	10
0935	21.5	8	7	24	29.0	29	5	10	29.0	3	0	14	27.0	0	2	10
0950	—	8	5	18	29.5	28	4	9	28.0	0	0	14	28.0	0	0	9
1005	21.5	8	2	32	30.0	23	4	12	29.5	0	0	13	27.5	0	1	8
1020	—	8	2	39	31.5	25	6	18	30.5	1	0	14	28.5	0	1	8
1035	23.0	9	8	13	32.0	24	8	10	31.0	0	0	10	27.5	0	0	11
1050	—	10	6	17	33.0	21	4	15	31.0	0	0	12	30.5	0	1	9
1105	24.0	9	11	4	33.5	22	6	13	32.0	0	1	14	29.0	0	0	10
1120	—	10	7	12	35.0	16	9	17	33.0	0	0	11	26.5	1	3	7
1135	25.5	11	3	16	29.5	15	6	14	33.0	0	0	9	27.0	2	3	9
1150	—	10	2	13	30.0	15	8	15	34.0	3	3	7	28.0	2	5	5
1205	26.0	11	2	10	31.0	16	5	15	34.5	5	4	12	28.5	2	4	8
1220	—	11	3	15	35.5	15	4	16	35.0	11	5	8	29.0	2	5	9
1235	27.5	10	3	16	32.0	14	6	15	35.0	19	9	4	29.5	2	5	8
1250	—	10	3	9	31.0	12	2	15	36.0	19	9	5	29.0	1	6	8
1305	27.0	9	3	12	31.0	12	3	17	31.5	20	3	14	28.0	2	4	8
1320	—	9	2	11	31.0	14	4	21	30.0	19	5	14	23.5	2	3	10
1335	27.0	14	3	8	30.5	15	2	17	30.0	23	5	8	23.0	2	4	12
1350	—	17	5	8	30.0	14	2	20	28.5	24	4	13	23.5	2	2	10
1405	27.0	14	3	11	29.5	11	3	20	30.0	28	7	10	26.5	4	5	6
1420	—	14	2	9	31.5	13	3	13	27.0	33	7	4	27.0	5	6	2
1435	24.0	16	2	33	33.0	15	4	12	27.0	37	6	10	27.5	4	7	2
1450	—	15	2	21	32.0	17	5	10	31.0	34	5	9	28.0	2	6	6
1505	24.0	13	2	16	34.0	18	3	14	32.5	35	8	3	29.0	3	4	8
1520	—	13	2	12	32.0	18	4	15	29.0	38	8	3	29.0	3	4	5
1535	25.0	12	3	5	31.0	18	2	16	29.0	37	7	2	28.0	3	1	9
1550	—	13	2	11	30.0	18	2	11	29.5	39	7	3	27.0	3	1	8
1605	25.0	12	2	12	27.0	15	2	13	28.0	40	7	3	26.5	2	1	10
1620	—	14	0	12	28.0	15	2	17	29.5	38	7	4	27.0	2	0	14
1635	24.5	11	1	13	27.0	14	2	19	29.5	39	8	3	26.5	2	0	13
1650	—	13	1	9	26.5	13	2	15	30.0	38	7	4	26.5	2	0	11

At Fajao O.P. similar observations were made over dawn and dusk, and midday periods, on the 14th and 15th July, respectively ; from 0600 to 1445 hrs. on the 16th July, 1956, and from 0700 to 1700 hrs. on the 5th January, 1957. Owing to distance and difficulties of terrain, counts of crocodiles in the water, where recorded, include only those seen swimming at the surface. It is not claimed that records of crocodiles seen ashore from this post include all that were present ;

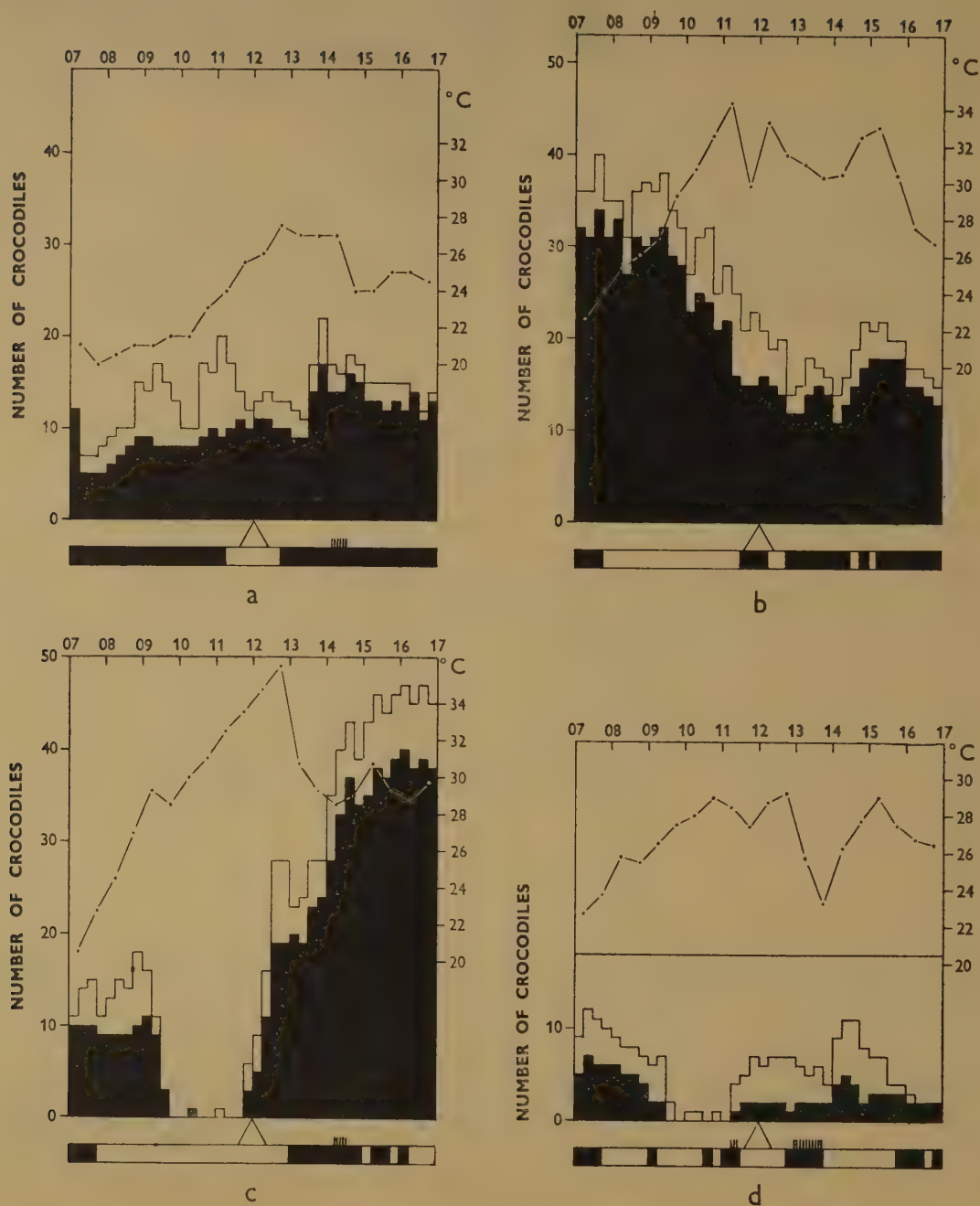


Fig. 3. Murchison O.P. (a) 8.7.56 ; (b) 10.7.56 ; (c) 12.7.56 ; (d) 4.1.57. Number of crocodiles counted per quarter-hour periods : black histogram—crocodiles lying ashore ; white histogram—crocodiles lying partly in and partly out of the water ; above—the greatest number of crocodiles counted in the water during any observation period. The lower strip indicates insolation ; white—clear sky ; black—overcast ; grid—rain. Shade temperatures are shown in the graph.

but errors of omission would be spread over all observation periods and so would not materially affect the observed pattern of activity (see Table 3 and Fig. 4, a to c).

These observations and the light they throw upon behavioural thermal control are discussed in the following section.

TABLE 3

Data for observation periods at Fajao O.P.; showing the number of crocodiles counted : *L*—lying ashore ; *P*—with part of the body in the water ; and *W*—in the water.

14.7.56			16.7.56				5.1.57				
<i>Time</i>	<i>Temp.</i>	<i>L.</i>	<i>Time</i>	<i>Temp.</i>	<i>L.</i>	<i>P.</i>	<i>Time</i>	<i>Temp.</i>	<i>L.</i>	<i>P.</i>	<i>W.</i>
0550	17.5	9	0605	18.0	33	17	0705	22.5	48	6	4
0605	19.0	27	0635	18.5	62	20	0720	22.0	58	2	1
0620	18.0	50	0705	20.0	75	20	0735	21.5	51	4	3
0635	18.5	56	0735	23.0	96	16	0750	22.0	48	6	2
0650	19.0	58	0805	24.0	100	20	0805	23.0	48	5	1
0705	20.0	69	0835	24.0	107	19	0820	24.0	42	7	3
0720	20.5	70	0905	25.0	114	25	0835	25.0	42	5	7
0735	22.0	78	0935	26.5	121	26	0850	25.5	38	5	4
0750	24.0	94	1005	27.0	77	24	0905	25.0	40	9	5
0805	24.0	89	1035	27.5	51	34	0920	26.0	39	9	9
0820	25.5	103	1105	29.5	55	38	0935	26.0	34	7	9
0835	27.0	105	1135	28.0	65	43	0950	28.0	33	9	2
—	—	—	1205	29.0	77	52	1005	28.0	28	10	6
1620	27.5	158	1235	30.0	83	55	1020	28.0	20	7	9
1635	27.0	141	1305	27.0	112	55	1035	29.0	12	9	11
1650	26.5	149	1335	27.0	133	58	1050	30.0	12	12	16
1705	26.0	149	1405	27.0	132	68	1105	29.5	10	10	8
1720	25.5	143	1435	28.5	131	66	1120	30.0	9	8	10
1735	25.0	116					1135	30.5	8	6	13
1750	25.0	115					1150	30.5	6	6	11
1805	25.0	94					1205	31.5	8	7	11
1820	24.5	84					1220	30.0	8	6	15
15.7.56							1235	33.0	6	5	13
1135	29.0	38					1250	33.5	9	6	24
1150	29.5	30					1305	33.0	3	14	13
1205	30.0	26					1320	32.0	15	8	16
1220	28.5	29					1335	31.0	18	8	16
1235	30.5	33					1350	30.0	19	7	18
1250	30.0	36					1405	32.5	30	7	16
							1420	33.0	40	7	18
							1435	30.5	45	6	9
							1450	31.0	43	6	9
							1505	31.5	44	8	7
							1520	31.5	44	8	12
							1535	31.0	43	5	17
							1550	30.5	53	5	14
							1605	29.0	55	5	13
							1620	29.0	55	4	11
							1635	29.0	55	4	10
							1650	28.0	54	4	11

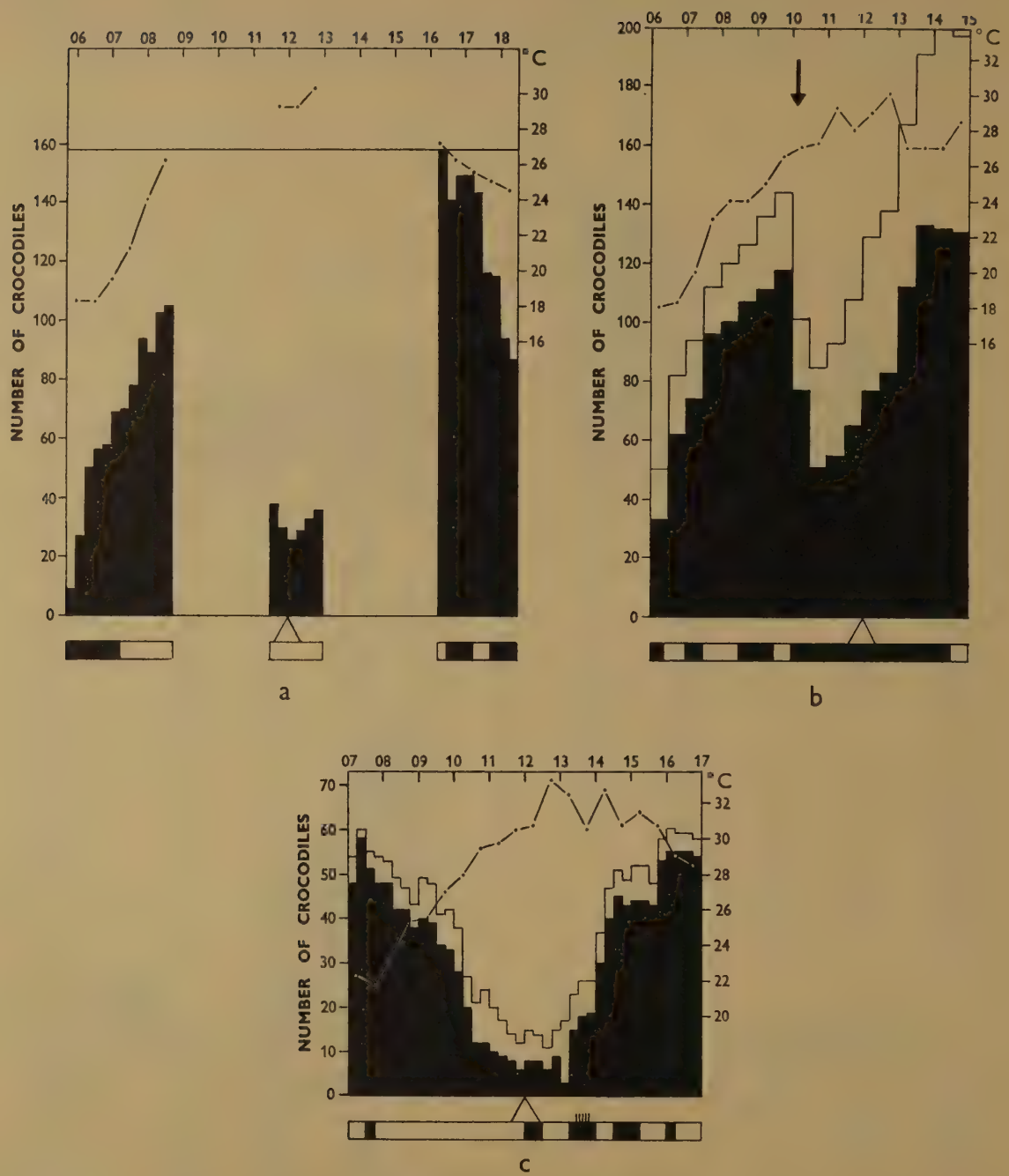


Fig. 4. Fajao O.P. (a) morning and evening, 14.7.56; midday, 15.7.56; (b) 16.7.56; (c) 5.1.57. Data are recorded as in Fig. 3. The arrow in (b) indicates disturbance caused by the arrival of a launch.

THERMOREGULATION

Many physiological experiments have been carried out with large reptiles—such as those by Isserlin (1902), Benedict (1932), Herter (1940), Colbert, Cowles & Bogert (1946) and Kirk & Hogben (1946)—to investigate the influence of thermal and other environmental factors upon body temperature. But the laboratory cannot reproduce the varied conditions obtaining in the natural habitat; and as Bogert remarks, the ways of controlling temperature in these tests are available to the experimenter but not to the animals used. In nature the reverse is true: a wild crocodile is free to choose conditions which meets its immediate and varying thermal requirements.

The present observations demonstrate the important part played by habitat selection and behavioural adaptation in the free-living animals.

Body temperature of crocodiles

Cloacal temperatures of crocodiles recorded immediately after they had been shot are given in Table 4. Although the sample is too small to indicate reliably the thermal range, yet the records—taken as they are from animals shot under widely different conditions, and by day and night—point to a remarkable degree of thermal control.

TABLE 4

Date	Locality	Serial No.	Sex	Length in m.	Place	Time	Temperature			
							cloaca	air, shade	substratum	water
6. 8.56	Magungu, Victoria Nile	109	♂	3.69	mud-bank in sun	1000	29.0	26.0	44.0	—
17. 8.56	Kinweshewa lagoon, Bangweulu	110	♀	2.48	water	2030	23.0	—	—	20.0
2. 1.57	Magungu, Victoria Nile	223	♂	4.22	mud-bank in shade	1000	26.5	27.0	—	27.0
5. 8.57	Musukwe lagoon, Lunsemfwa Valley	258	♀	2.15	water	2000	24.8	19.3	—	22.8
31. 8.57	Iyeshya, Kafue Flats	395	♀	2.82	water	2000	24.8	—	—	21.8
31. 8.57	Iyeshya, Kafue Flats	396	♂	2.86	water	2300	26.3	15.0	—	21.5
19. 5.58	Luangwa River	At.1	♀	2.32	bank	0845	25.0	19.8	—	25.8

The series shows a mean temperature of 25.6°C . and a range of 6 degrees, with fluctuations from the mean of $+3.4$ and -2.6 degrees. The mean temperature of specimens shot on land is 26.8°C . and that of specimens shot in the water is 24.7°C .

*Behavioural control**The environment*

The crocodile's environment includes many thermal factors which vary in time and space. Mean water and air temperatures recorded at Murchison are as follows:

time	.	.	24	03	06	09	12	15	18	21	24	hrs.
water	.	.	23.5	23.5	24.0	24.5	25.0	25.0	24.5	24.0	23.5	C.
air, shade	.	.	19.0	19.0	18.7	24.8	29.3	29.0	23.4	21.5	19.0	C.

The water readings were taken at a depth of one foot off the end of Fajao jetty : air temperatures are the means of recordings taken during July and January. It will be seen that the thermal levels of air and water are transposed twice every twenty-four hours.

Heat exchange between the body and substratum will be influenced by the latter's conductivity index, and by moisture, texture and contained shadow, which will differ for surfaces of bare rock, sand and earth, grass or lush vegetation. Effects of insolation will vary with the weather and time of day, and with orientation of the reptile in relation to the sun. Rate of evaporation from the body when wet after rain or recent emergence on land, and from the mucosa when the jaws are agape, will be affected by wind-force and relative humidity.

Superimposed upon these variables are the movements, rhythmic or sporadic, of the crocodiles themselves, between land and water, sun and shade. These movements are certainly to be interpreted in terms of thermal requirements.

Diurnal movements

Early morning basking evidently plays an important role in the restoration of heat lost during the night (Plate 2, fig. 1). In field studies of agamid lizards, Cowles (in Curry-Lindahl, 1956-7) has shown that solar radiation is far more important than air temperature as a source of heat. And it is to be noted that the early morning exodus of crocodiles to land begins long before the air temperature has risen to that of the water they have left.

The time of the early morning haul-out varies at the same place from day to day, apparently in relation to prevalent weather. For example, on a cool day a favourite sand-bank near Fajao was still vacant at 0545 hrs., and was tenanted by only one crocodile at 0630 hrs.: on that morning the shade temperature did not reach 20° C. until 0730 hrs. At the same spot on the following morning, when the shade temperature was 20° C. at 0600 hrs., six crocodiles were already ashore and three half-out at 0545 hrs.

Despite lack of proof, it seems evident that crocodiles bask until the body temperature has been raised to a point near the upper limit of the normal activity range. Thereafter, they crawl into shade, lie at the water's edge, or enter the water and so dissipate heat. Thus, on a cloudy day with relatively low temperatures (8th July—see Fig. 3 a) there was no typical return to the water around midday, such as was seen when the rocks had been long exposed to insolation (10th July—see Fig. 3 b).

The combined effect of prolonged insolation and high temperature is strikingly seen in the movements recorded on 12th July (see Fig. 3 c), when the shade temperature rose to 36° C. The ground temperature on the rocks is not known, but 58° C. was recorded at bulb-depth in the sun at the O.P. For about two hours the islets were entirely deserted.

Observations on orientation of basking crocodiles in relation to the direction of the sun—such as have been recorded for *Phrynosoma modestum* (Wesse, 1917)—are not available. But there can be no doubt that the reptile's habit of lying for

long periods on a bank with part of the body submerged provides an effective means of adjusting the area of the body exposed to the sun (Plate 1, fig. 2, and Plate 9, fig. 2).

In the late afternoon the trends seen in the early morning are reversed, and by returning to the water before sunset the reptiles escape the low air temperatures and conserve their heat during the night in the warmer medium.

Size and thermoregulation

Size is an important factor in an animal's thermal relations with its environment. The larger the animal, the lower is its surface-to-bulk ratio and the greater its capacity for heat storage. In studies of temperature tolerance in a graded series of thirteen alligators, Colbert, Cowles & Bogert (1946) have demonstrated that during exposure to the sun, the rate of heat absorption is inversely proportional to the animal's bulk. The same relationship applies to the rate of heat loss.

Experiments by Kirk & Hogben (1946) have shown that when young alligators about a metre long and weighing 4 kg. were exposed to a sudden drop in temperature of 20° C., ten hours elapsed before the body temperature fell approximately to that of the chamber. The much greater bulk of an adult crocodile will greatly retard this cooling process—thus enabling it to maintain its thermal level within the normal activity range at night. Heat loss at night will also be countered by the heat produced in muscular exertion—for example, when the animal is actively swimming in search of prey.

When the crocodile is subjected to high temperatures in the day time, changes in the body temperature will again follow only sluggishly. The stabilising effect of bulk may be illustrated by an example. At the Murchison O.P. on 8th July a large male was observed to remain motionless, lying with its tail in the water and its body on the rocks, for a period of over nine hours (from 0705 to 1620 hrs.). Such sedentary behaviour is in striking contrast to the restless activity of tropical agamids in which voluntary exposure to the sun does not exceed twenty minutes at a time (Curry-Lindahl, 1956–7).

Mouth gaping

When they are lying ashore or partly submerged by day, crocodiles are commonly seen with the jaws held widely agape (Plate 2, fig. 2). The effect of this habit upon body temperature has not been directly demonstrated in *C. niloticus*. But from indirect evidence there can be no doubt that exposure of the moist mucosa does provide, through evaporation, an important accessory cooling mechanism.

(a) Behaviour analogous to mouth gaping in the crocodile is known among birds. For example, in hot weather and when exposed to insolation on the nest, gannets (*Sula bassana*), shags (*Phalacrocorax aristotelis*) and cormorants (*P. carbo*) commonly open the bill and rapidly vibrate the gular pouch. Similar behaviour is seen in the African *P. lucidus* and *africanus*. That gaping and fluttering of the

throat is an efficient behavioural adaptation for the dissipation of heat has been clearly demonstrated by Cowles & Dawson (1951) in their studies of the Texas nighthawk (*Chordeiles acutipennis*).

(b) It is known that if a crocodile is restrained in direct sunlight with its jaws roped together, its temperature rises beyond the normal activity range and death ensues. Shelford (1916) states that this was in fact the normal method he used to kill specimens of *C. porosus* that were brought to the museum.

(c) Colbert, Cowles & Bogert (1946) have demonstrated experimentally that alligators are able to maintain the body temperature for a long time, even when this approaches the critical maximum (about 38° C.) ; that the method of control is by loss of water through evaporation ; and that this loss—which may during twenty-four hours amount to as much as 20 per cent. of the body weight—is regained by absorption when the alligator is replaced in water.

(d) Further evidence is afforded by field studies of *C. niloticus* in Uganda. During routine observations records were kept to show, for crocodiles lying ashore, (i) the time of day, (ii) insolation, i.e. exposed, or shaded by cloud or cast shadow, and (iii) posture, i.e. jaws gaping or closed. Table 5 contains an analysis of these data arranged in hourly periods.

TABLE 5

Mouth-gaping in relation to time of day and to insolation : showing, for hourly periods, the number of crocodiles seen ashore with the mouth closed, and open.

Time	In sun			In shade			Total % Open
	Closed	Open	% Open	Closed	Open	% Open	
0500-0600	—	—	—	6	?	0·0?	0·0
0600-0700	9	4	30·8	11	3	21·4	25·9
0700-0800	129	85	39·7	170	65	27·7	33·4
0800-0900	223	212	48·7	49	10	16·9	44·9
0900-1000	124	243	66·2	37	7	15·9	60·8
1000-1100	60	145	70·6	44	20	31·3	61·3
1100-1200	57	86	60·1	39	39	50·0	56·6
1200-1300	81	111	57·8	45	40	47·1	54·5
1300-1400	11	28	71·8	145	116	44·4	48·0
1400-1500	66	98	59·8	166	160	49·1	52·7
1500-1600	121	132	52·2	158	99	38·5	45·3
1600-1700	200	56	21·9	110	52	32·1	25·8
1700-1800	1	0	0·0	9	0	0·0	0·0

It will be seen from Fig. 5 : (a) that the proportion with jaws agape tends to increase progressively during the morning when the external temperature is rising and to decline again with falling temperatures in the afternoon ; and (b) that the proportion of mouth gapers is generally higher, at any time of day, for crocodiles exposed to the sun than for those lying in shade.

During the heat of the day crocodiles frequently lie half out on shore, with

part of the body or with the tail submerged (Plate 9, fig. 2), and with the jaws gaping. The inference is that these animals are losing heat by evaporation from the mucosa and simultaneously making good the loss of body-fluids by absorption through the submerged surfaces.

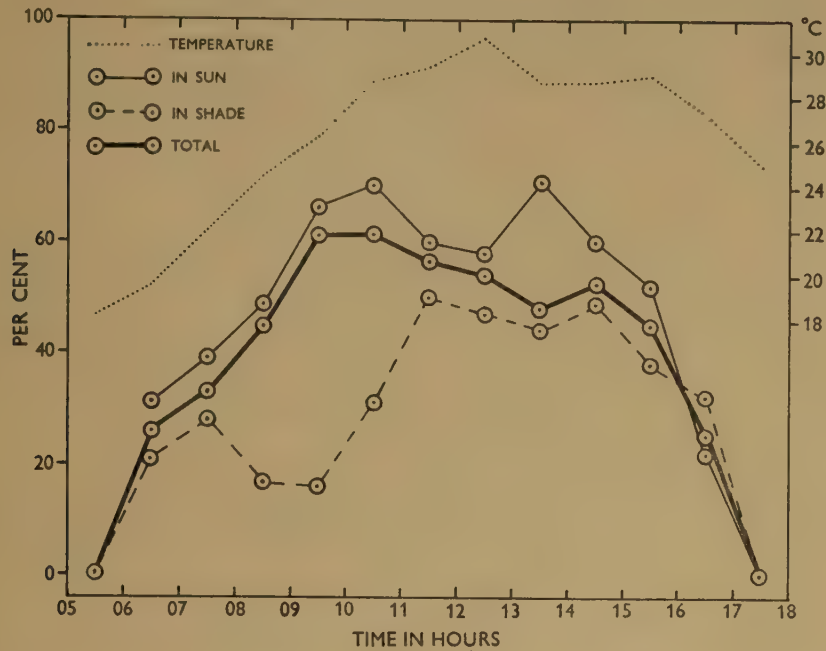


Fig. 5. Diurnal variation in mouth-gaping. The number of mouth-gaping individuals is expressed as a percentage of all crocodiles seen lying ashore; thin line—individuals exposed to the sun; broken line—those in shade; thick line—total. Mean shade temperatures are shown above.

Taken together, the foregoing observations indicate that by habitat selection and behavioural adaptation crocodiles are able to exercise a remarkable degree of control over the thermal level of the body. Indeed, they afford an extreme example of the approach, made by an ectotherm, towards endothermal life.

TERRESTRIAL LOCOMOTION

Although about half a crocodile's life is spent ashore, during most of this time the animal lies sprawling, lazy and inert. From long observation in the field one gains the impression that crocodiles, and especially older animals, are most reluctant to carry their weight on land, and that terrestrial locomotion is a labour to be undertaken only in emergencies or in relation to the requirements of thermo-regulation. The mastery of terrestrial travel in no way compares with the grace and ease of movement in the water, which is the crocodile's real environment—both as a feeding ground and place of refuge.

When moving on land the crocodile has three distinct gaits. These may be described as the high walk, the belly run, and the gallop.

The high walk

This is the normal gait, and is the method of progression always seen when a crocodile is hauling its weight out onto the rocks or up a river bank. The high walk is also used in unhurried overland travel, for example, when a crocodile is going to its nest, or returning from the basking grounds to the water.

At such times the animal goes, not like a lizard with the legs splayed out sideways, but like a leopard, the legs swinging beneath the body and so carrying the belly high off the ground. The sacrum is held higher than the shoulder, the head is somewhat declined, and the back arched, only the lower surface of the tail-tip trailing (Plate 1, fig. 1, and Plate 3, fig. 1).

In this type of plantigrade locomotion, the legs move in diagonal pairs—the left fore and right hind legs coming forward together, to be followed by the right fore and left hind legs. At each stride two legs are on the ground and two in movement; and at the end of each stride the hind foot is placed close behind the fore foot of the same side, before the latter has been lifted to continue the sequence. The locomotory pattern, though not the swinging pace, is similar to that seen in the loping trot of a large cat.

When an adult crocodile is travelling up-hill, across country, or over broken terrain, such a means of locomotion is clearly related to the animal's great bulk, which could not be forced along the ground if the limbs were splayed sideways with the chin, belly and tail dragging. During the high walk the longer and stronger hind limbs, which have their origin not far behind the centre of gravity, take most of the weight, while the slender and shorter fore limbs act as props to support the head and shoulders. In going up-hill the animal's weight appears to be sustained almost entirely by the hind limbs as they haul the body upward and onward, the fore legs merely acting as mobile struts.

The belly run

When disturbed ashore a crocodile's immediate reaction is to make for the water at speed. The gait employed will then depend upon circumstances. If level ground has to be traversed crocodiles will make for cover, the run in this case being merely an acceleration of the high walk. But the way to the water generally lies down-hill. Then, and especially when hard pressed to make their escape, crocodiles adopt the belly run or scuttle.

In this gait the animal reverts to the crawling posture, and slides or toboggans over the ground, its polished ventral shields acting like the undercarriage of a sleigh, and the motive power being provided partly by gravity and partly by the action of the legs which are spread laterally like oars to propel the body forward (Plate 3, fig. 2). The belly run is much faster than the high walk, and is used not only on grassy or sandy slopes, but on precipitous rock descents. At Kigi I have seen crocodiles racing in this way from a height of forty or fifty feet, to hit the water with tremendous impact.

The gallop

The third gait is one that has very rarely been observed, and has not previously been recorded. In the gallop, the fore legs and hind legs work together in serial pairs. The body is carried forward by the backward thrust of both hind limbs while the fore limbs are extended to take the impact. The hind limbs are then brought forward beneath the belly during the backward thrust of the fore limbs. The leg action is rapid, the crocodile bounding along like a squirrel, with a pitching motion of the body, and at an estimated speed of about 7 or 8 miles per hour.

During months of observation I witnessed the gallop only four times—near Fajao, Paraa and Magungu on the Nile, and at Butiaba, Lake Albert. On two of these occasions I was accompanied, respectively, by Capt. J. R. F. Mills and Major R. E. P. Wyndham. The habit is so remarkable—and indeed improbable—that I am glad to have confirmation of this locomotory pattern from independent observers. Mr John Savidge (12.2.57) has sent me an account of the gallop which he witnessed at Buligi; and Major B. G. Kinloch tells me he has also seen this unusual gait. The circumstances were generally similar in every instance. Crocodiles seen galloping have all been small specimens measuring between about one and two metres in length; and on each occasion the animals had been suddenly surprised in sleep when some distance from the water, and had broken into this strange bounding gait on waking to find themselves discovered at close range.

TRAVEL AND AESTIVATION

During the rains crocodiles often follow the flood waters as they spread over the plains. This was observed, for example, at Lake Nyamiti, Ndumu Game Reserve, Zululand, where in early November, 1956, many crocodiles were seen moving into the newly-inundated areas—either to follow fish or to find warmer water. These movements sometimes take the animals far from permanent water; and they get into pools where they are later marooned as the floods recede. Eventually, as the pool dries up, they attempt to regain the valley and are sometimes found moving overland far from water.

In Northern Rhodesia Major W. E. Poles (1956) came upon a seven-foot crocodile in the middle of an open plain about a mile and a half from the nearest lagoon. More remarkable is the instance reported by Trollope (6.7.54) to Player, from the Chobe River, where he met a crocodile travelling across country fifteen miles from the nearest water. Other records are given by Baker (in Anderson, 1898) and Cansdale (1955).

It is known that under such circumstances crocodiles can withstand drought by prolonged aestivation. In a tributary of the Dyoor River, Schweinfurth (1874) found crocodiles living in pools and puddles of the dry river bed where, as he says, "buried in the miry clay, they find a sufficiently commodious home."

In the Southern Province of Tanganyika, aestivation appears to be a regular habit. Mr G. H. Swynnerton told me that at Rukwa during the dry season the reptiles occupy roomy chambers which are reached by tunnels dug into the river

banks. Evidence that they remain a long time in these retreats is provided by the growth of ambatch shoots in the entrances. This habit is also confirmed by Mr B. D. Nicholson, who tells me that on the Songwe River, south Rukwa, as many as fifteen crocodiles have been found occupying one cavern. In their torpid state, such crocodiles can be clubbed, one at a time, and put up no fight. Nicholson also states that when the Mbwemkuru waters dry, crocodiles work their way into the wet mud and as this cakes and cracks above them they get further down into the damp zone, till they may be found buried, and lying straight extended, five feet below the surface. Thus they remain for the five months' dry period.

AQUATIC BEHAVIOUR

The Nile Crocodile has perfect mastery of aquatic locomotion. However, perhaps on account of respiratory difficulties, the reptiles are reluctant to move into open water far from land, and they are rarely seen far from shore in Lakes Albert and Victoria. Even so, the species is not even restricted to the fresh water habitat. Player tells me he has, on several occasions, encountered crocodiles at sea off St. Lucia, Zululand ; and that formerly a great number of crocodiles used to lie at the mouth of the estuary, where a fight between a crocodile and a shark was once witnessed. W. M. Austen informed Player that during the 1917 floods a very large crocodile was seen swimming north about seven miles out to sea off St. Lucia—the occurrence being entered in the log of S.S. *Kathinwar* by the master, Captain Harper.

Swimming

When in its normal fresh water habitat, the crocodile rarely exerts itself. In lagoons and other still waters the animals spend much of the time floating idly at the surface. In rivers they generally keep station against the current with leisurely tail strokes. Where the water is clear, as for example off the rock islets below Murchison, they can often be seen lying motionless on the bottom in three to six feet of water during the heat of the day.

Active swimming is effected entirely by lateral undulations of the powerful tail (Plate 4, fig. 1). The limbs take no part in propulsion, being closely applied to the flanks. A few observations on swimming crocodiles are given in Table 6. Most of these records refer to specimens that were cruising slowly to maintain their position against the current. In general, the sweep of the tail is slow, and for any given swimming speed, slower in large than in small specimens. But when wounded, or when about to capture prey, a crocodile can dart forward with a tremendous spurt of activity and indeed may sometimes leap right out of the water like a great fish.

Respiration

In the unruffled waters which they normally frequent, crocodiles float low, with little more than the nasal disc, eyes and occiput above the surface. Immediately

TABLE 6

<i>Date</i>	<i>Locality</i>	<i>Period of observation in seconds</i>	<i>No. of tail cycles</i>	<i>Cycles per minute</i>	<i>Activity</i>
9.7.56	Fajao	61	30	29.5	Keeping station in shore.
14.7.56	Fajao	82	39	28.5	Leisurely swimming in slack water.
15.7.56	Fajao	87	30	20.7	Station keeping in slack water.
15.7.56	Fajao	62	30	29.0	Rapid swimming (in part).
15.7.56	Fajao	87	50	34.5	Heading up river for bank against fast current.
18.7.56	Fajao	45	23	30.7	Cruising speed.
30.12.56	Magungu	60	16	16.0	Keeping station against slack current off grounds.
6.1.57	Murchison	50	25	30.0	Cruising speed.
6.1.57	Murchison	63	25	23.8	Slow cruising speed.

before a dive the nares are closed, and the animal sinks—presumably by contracting the thorax and abdomen and so increasing the specific gravity.

In calm weather a submerged crocodile needs only to break surface with the nasal disc in order to breathe. Broken water interferes with the normal procedure, and in rough weather the snout has to be raised well above the surface and at a steep angle during inspiration. The animal then slips back, like a foundering ship, and disappears. For this reason, crocodiles tends to avoid rough water. According to Pitman (1931) they are not found in surf such as prevails along the shores of Lake Rudolf. And I am informed by Holloway that in windy weather crocodiles will even come ashore at night: this is quite contrary to their habitual routine.

Submergence

Since the reptiles can momentarily appear at the surface, in cover and unnoticed, it is extremely difficult to obtain reliable field data regarding submersion periods, and little is known of an adult's diving endurance. Holloway told me that in 1955 when hunting at night in a tributary of the Chambezi River he came upon an eight-foot crocodile which dived at the approach of his boat and lay on the bottom in about four feet of clear water. He waited above the reptile for an hour, during which it did not move. Player made a similar observation at Ndumu, where he watched a crocodile lie submerged for an hour.

Observations on captive crocodiles have proved that even small specimens can remain submerged for surprisingly long periods.

Submersion tests

Submersion tests were carried out at Jinja with four small crocodiles—each being held below the surface by a loose-fitting, weighted harness. The

animals' reactions are summarized in Fig. 6. Numbers 1 and 3, both newly-hatched specimens, recovered after being submerged for thirty minutes. Numbers 2 and 4 failed to recover: but the latter (length 792 mm.) was still moving fifty-seven minutes after submersion, and would almost certainly have survived an hour's dive.

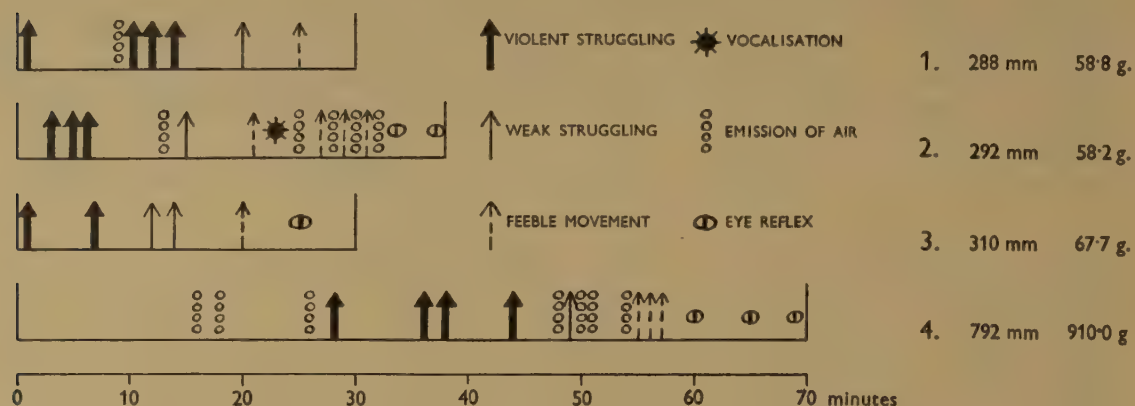


Fig. 6. Summary of activity of four crocodiles during submersion tests.

Diving times

In a second series of observations, a recently-hatched specimen, Jinja, 1952 (Number 1) and three larger specimens captured in Bangweulu Swamp, 1956 (Numbers 2, 3 and 4), were released in a pond—their diving and surfacing times being recorded over three- or four-hour periods. The results are summarized in Table 7; and the sequence of respiratory rhythm is shown in Fig. 7.

TABLE 7

Serial No.	Length in mm.	Period of observation	Total time surfaced		Total time submerged		No. of submersions	Mean submergence time		Max. submergence time	
			min.	sec.	min.	secs.		min.	secs.	min.	secs.
1	290	3 hours	94	0	86	0	12	7	10	16	0
2	661	4	48	20	191	40	17	10	27	25	30
3	982	4	2	24	237	36	13	18	17	35	15
4	992	4	3	12	236	48	15	15	47	44	0

The larger specimens from Bangweulu were very wary under observation and only surfaced momentarily for air before sinking again to the bottom. Some of the diving periods may therefore represent near maxima for specimens of the sizes given. In Fig. 8, the two longest diving times recorded for each of the four specimens are plotted against crocodile length. It will be seen that the maximum submergence times tend to vary in relation to size; and that the largest specimen

(measuring nearly one metre) was at one time submerged for forty-four minutes. If the trend here shown is maintained into the higher length-groups, then the maxima for adults would be far in excess of the one-hour periods that have been recorded in the field.

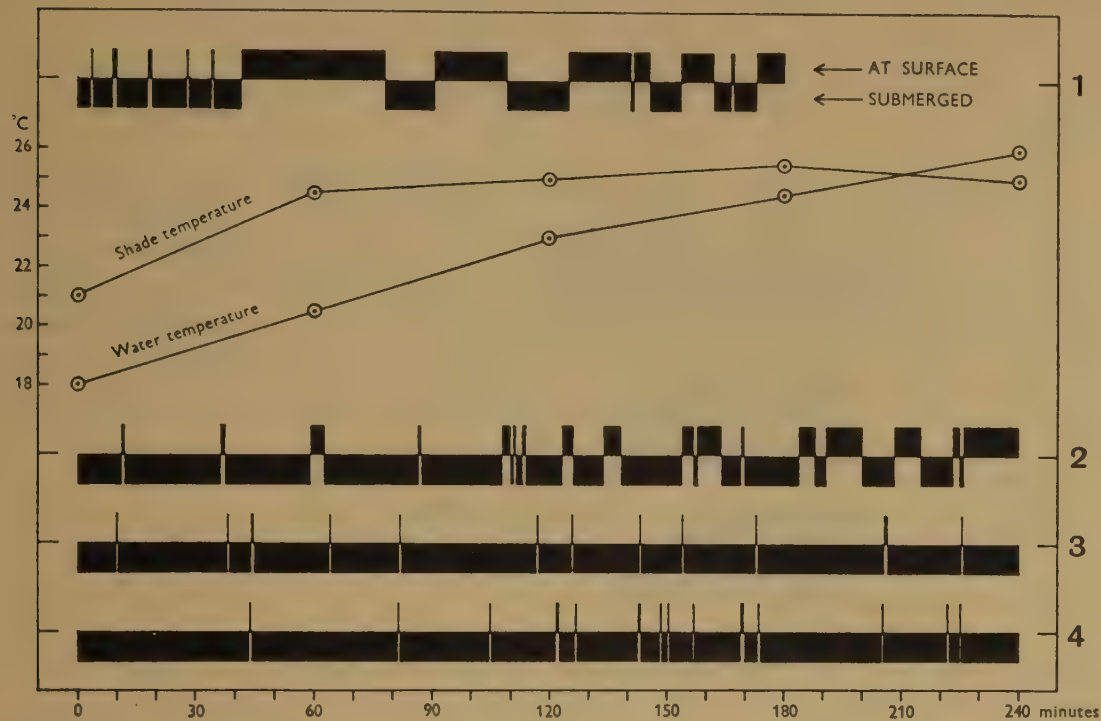


Fig. 7. Diagrammatic representation of the respiratory activity of four crocodiles, measuring: 1-290 mm. (Jinja); 2-661 mm., 3-982 mm. and 4-992 mm. (Samfya). The indicated shade and water temperatures refer to the observations at Samfya, L. Bangweulu.

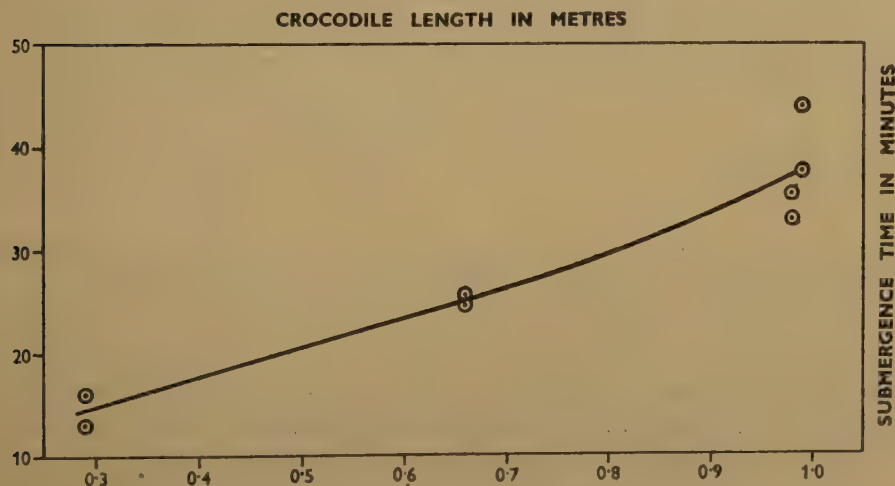


Fig. 8. Graph showing the relation of maximum submergence periods to crocodile length.

STOMACH STONES

The presence of stones in the stomach of crocodiles has often been reported, and commented upon ; but hitherto the mode of occurrence of the stones themselves—as an essential basis for an enquiry into their possible function—has not been systematically studied.

*Occurrence and weight**Material*

The following summary is based upon data for occurrence of stones (presence or absence) in 681 crocodiles, examined in Uganda and Northern Rhodesia. Most of these were examined by the writer ; but additional records received from Mr F. Wilson (23), Mr H. Holloway (45) and Mr H. H. Voigt (66) are here included. The material was examined in the following localities : Lake Victoria (84) ; Victoria Nile (27) ; Lake Kioga (4) ; Lake Albert (15) ; Semliki R. (2) ; Bangweulu Swamp (84) ; Mweru Wa Ntipa (41) ; Kalungwishi R. (12) ; Luangwa Valley (96) ; Kafue Flats (89) ; Upper Zambesi (227).

Further data relating to crocodile weight and weight of stones carried are available for 507 crocodiles from the same localities.

Occurrence of stomach stones

Data relating to occurrence of stones, in relation to crocodile length, are as follows :

Length in metres ..	0.3+	0.5+	1.0+	1.5+	2.0+	2.5+	3.0+	3.5+	4.0+	4.5+
No. examined	10	122	116	96	97	105	82	31	15	7
No. containing stones	0	61	78	79	87	105	82	31	15	7
Per cent.	0	50	67	82	90	100	100	100	100	100

Apart from very rare exceptions, it is true to say that crocodiles never carry stones during the first year of life, and that they have always acquired them before reaching maturity. Within these limits, the period of initial intake differs widely according to locality. For example, stones were present in the stomachs of *all* eighteen crocodiles in the 0.75 to 1.0 metre group from the Luangwa Valley ; whereas from Bangweulu Swamp none were found in twelve crocodiles below 1.5 metres in length, and only four out of eleven in the 1.5 to 2.0 metre group contained stones.

The fact that the Luangwa Valley is stony, and Bangweulu Swamp stoneless, suggests that availability of mineral matter is the explanation of such differences. This explanation may be tested by an analysis of the data in relation to three main types of habitat : (a) rivers and lakes with stone-strewn shallows and shores (Lakes Albert and Victoria, Victoria Nile, Kalungwishi, Lunsemfwa and Luangwa Rivers) ; (b) meandering rivers, flowing through alluvial plains, with a bottom of sand or mud (Lower Semliki, Kafue Flats and Upper Zambesi) ; and (c) virtually stoneless swamps with a bottom of ooze and detritus (Kioga, Bangweulu and Mweru Wa Ntipa).

The occurrence of stones, expressed as a percentage of crocodiles of different length-groups examined from these three classes of habitat, is shown graphically in Fig. 9. Thus analysed, three patterns are seen—both as regards (i) the growth-stage at which stones are first ingested by individuals; and (ii) the length-group above which the whole population becomes stone-bearing.

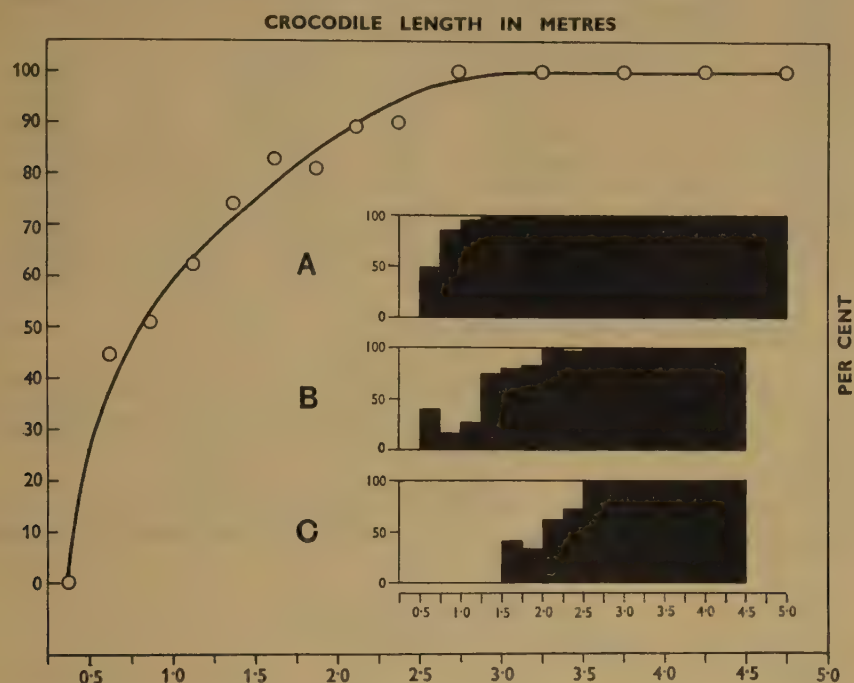


Fig. 9. Occurrence of stomach stones, expressed as a percentage of crocodiles examined in each length group. Inset—percentage occurrence of stones in stomachs of crocodiles taken in different habitats: A—stony; B—meandering river; C—swamp.

In stony habitats intake is early and rapid, being complete for the population at the 1.26 metre size. In alluvial flats, though a few crocodiles acquire stones early in life, at about 1.25 metre length only one in four contains stones, and the process of initial intake extends into the 1.75 to 2.0 metre group. In the swamp crocodiles, intake does not begin below 1.63 metres, and occurrence only reaches finality in the 2.25 to 2.50 metre group.

Weight of stomach stones

Data relating to weight of stones carried by crocodiles of different sizes are summarized in Table 8.

The results will be briefly discussed here under two heads: (i) the absolute weight of stones per stomach; and (ii) the weight of stones in relation to crocodile weight.

(i) *Absolute weight.*—Data for the combined collections show that the mean weight of contained stones increases progressively with age, from zero in the smallest length group to 3356 g. in the largest. (The greatest absolute weight is that recorded for No. 30, a male of 4.71 metres from Magungu, which contained 4766 g. of stones.)

TABLE 8

Stone weight in relation to crocodile length, showing maximum, mean and minimum values, and the weight of stones expressed as a percentage of the body weight.

Length group (metres)	Number of stomachs examined	Mean body weight (kg.)	Stone weight (gm.)			
			Max.	Mean	Min.	Percent.
0.3-0.5	10	0.146	—	0.0	—	0.0
0.5-1.0	101	1.524	16	2.044	0	0.134
1.0-1.5	102	4.518	125	11.70	0	0.259
1.5-2.0	76	16.54	480	88.87	0	0.537
2.0-2.5	73	40.90	980	312.5	0	0.764
2.5-3.0	69	79.39	2160	700.3	7	0.882
3.0-3.5	52	131.9	4540	1321.2	30	1.002
3.5-4.0	16	206.5	5100	1906.2	620	0.923
4.0-4.5	5	298.7	3600	2940.4	1450	0.984
4.5-5.0	3	325.5	4766	3356.0	2179	1.031

Specimens taken in different localities show a generally similar pattern of increase, which tends to be gradual in the lower, and to rise steeply in the higher length-groups (Fig. 10).

(ii) *Relative weight*.—When plotted against crocodile length, the mean relative weight of stones (expressed as a percentage of the mean body weight) is represented

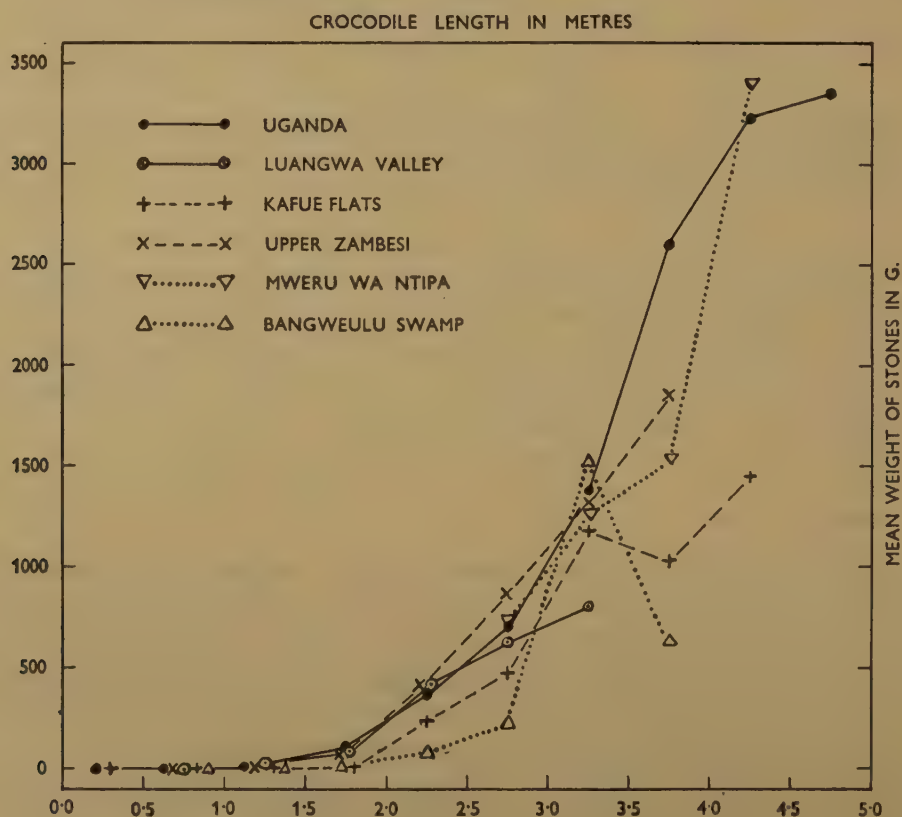


Fig. 10. Mean weight of stomach stones in relation to crocodile length, for six localities.

by a sigmoid curve which flattens out at a value of approximately one per cent. This may be regarded as the "standard load" for adult crocodiles.

Table 9 gives an analysis of the data for females and males separately ; and in Fig. 11 the values for mean stone weight are plotted as a percentage of the

TABLE 9
Data for stone weight in relation to sex.

Length group	Males				Females			
	Size of sample	Mean crocodile weight	Mean stone weight	Percent. stone body	Size of sample	Mean crocodile weight	Mean stone weight	Percent. stone body
metres		kg.	gm.			kg.	gm.	
0.3-0.5	2	0.22	0.0	0.0	—	—	—	—
0.5-1.0	45	1.60	1.65	0.103	47	1.52	2.51	0.165
1.0-1.5	49	4.57	12.94	0.283	52	4.41	10.30	0.234
1.5-2.0	35	17.20	105.7	0.615	40	16.16	75.93	0.470
2.0-2.5	34	40.87	270.7	0.662	39	40.92	348.9	0.853
2.5-3.0	32	74.99	619.9	0.827	37	82.94	769.8	0.928
3.0-3.5	18	131.2	1189.9	0.907	34	132.3	1390.7	1.051
3.5-4.0	16	206.5	1906.2	0.923	—	—	—	—
4.0-4.5	5	298.7	2940.4	0.984	—	—	—	—
4.5-5.0	3	325.5	3356.0	1.031	—	—	—	—

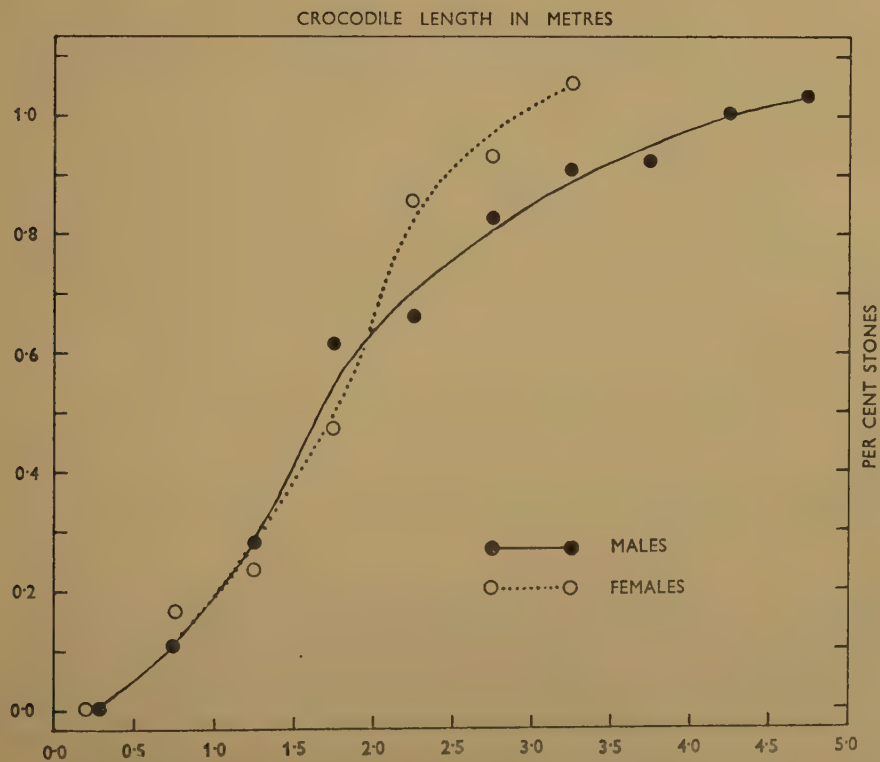


Fig. 11. Mean weight of stomach stones, expressed as a percentage of the mean body weight, in relation to crocodile length and sex.

body weight. The curves for the two sexes show the same characteristics—though they become horizontally displaced in the higher length-groups owing to sexual disparity in adult size (see p. 252). On attaining sexual maturity the length of females is about 2·4 to 2·8 metres, that of males about 2·9 to 3·3 metres. The values indicated by the smoothed graphs under these length-groups are close, being 0·88 to 0·97 for females, and 0·83 to 0·89 for males. Thereafter, the curves for large crocodiles of both sexes tend to level off at the standard load of about one per cent.

Further analysis of the data, in terms of the three types of habitat previously referred to (p. 236) is shown graphically in Fig. 12. Different availability of stones in stony, meandering and swamp waters seems to be the factor responsible for the marked differences seen under the lower length groups. The curves for crocodiles in stony and alluvial habitats are the first to converge with growth, and for the

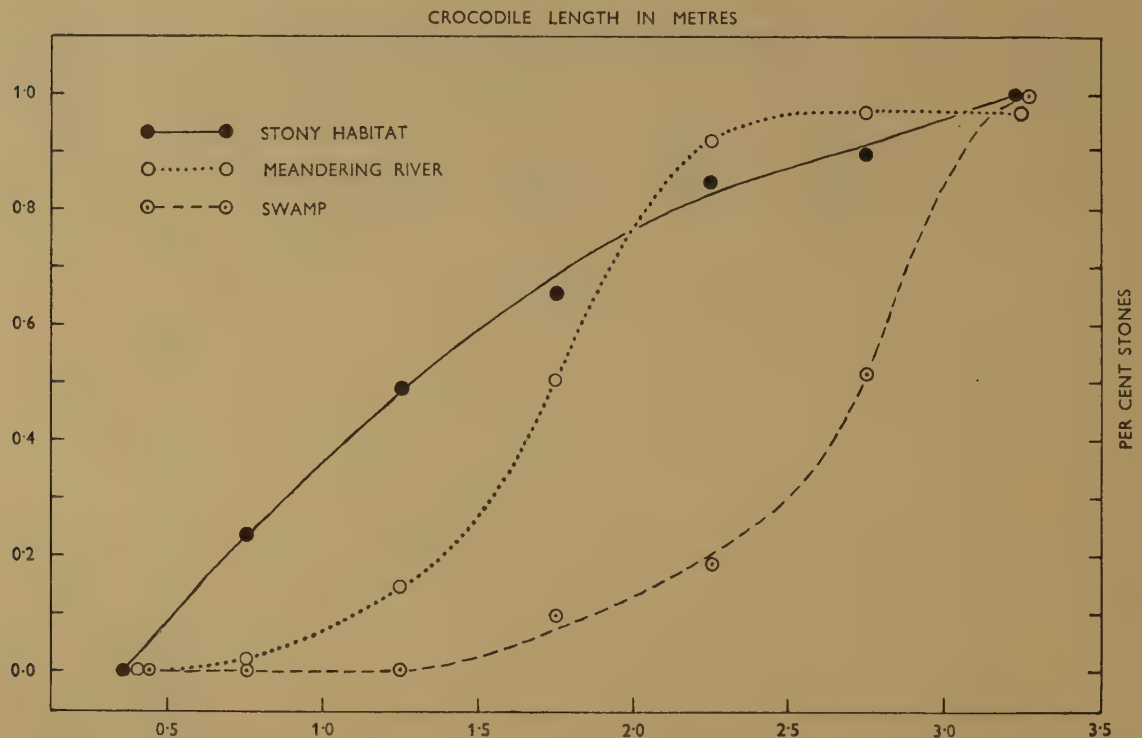


Fig. 12. Mean weight of stomach stones, expressed as a percentage of the mean body weight, in relation to crocodile length and habitat.

length-group above 1·5 metres they run approximately together. Swamp crocodiles lag behind in their intake : those in the 2·5 to 3·5 metre group still carry only about half the relative weight found in crocodiles of comparable size from other habitats. Yet the remarkable fact emerges that the relative weight of stones carried by mature crocodiles living in a virtually stoneless terrain eventually increases to conform with the general pattern, until in the 3·0 to 3·5 metre group (the largest for which adequate swamp records are available) the graphs converge.

The relevant figures for this length-group are as follows :

Habitat where shot			Stony habitat	Meandering river	Swamp
Size of sample	14	27	11
Mean body weight, kg.	137.9	132.4	123.2
Mean stone weight, gm.	1377.0	1281.0	1350.0
Percent, stones/body	0.999	0.968	1.096

The significance of the standard load of stones, found in adults of both sexes, and from every type of terrain, is discussed below.

Acquisition of stones

The circumstances under which crocodiles acquire pebbles are not certainly known. There appear to be three possible explanations : (a) that stones are accidentally ingested ; (b) that they are adventitiously derived from the stomachs of prey ; or (c) that they are deliberately swallowed. All the evidence now available points to the third explanation as the only satisfactory one.

(a) The distribution of stones throughout the populations, and the quantity found in individuals, render the first hypothesis unlikely. (i) Many juveniles have already acquired pebbles when they are still feeding in weedy shallows. (ii) Adults living in almost stone-free swamps contain approximately the same mean weight of stomach stones as others, of comparable size, living in stony habitats. (iii) Very old crocodiles do not carry a disproportionately large cargo of stones.

(b) Secondary derivation from the bodies of prey cannot be supported by evidence. (i) Young crocodiles commonly carry stones at a period when they are still feeding on prey (invertebrates and amphibia) which could not contribute stones. (ii) The victims of older crocodiles could scarcely supply the demand. For example, of 300 *Pelecaniformes* of five species examined by the writer in Uganda, only one contained one small pebble. Mr P. H. Greenwood tells me (22.12.57) that he has found *no* stones in any *Bagrus*, *Clarias*, *Synodontis*, *Protopterus*, *Barbus*, *Tilapia* or *Haplochromis*. The only other source under this head would be via cannibalism, which obviously cannot account for the stone-carrying habit.

(c) The third supposition, that stones are voluntarily ingested, finds indirect support from what has been said above, and also from the following considerations. Crocodiles living in virtually stone-free waters must of necessity make extensive journeys to collect their mineral load. For example, specimens from Bweramule, on the Semliki, were shot miles from any known source of supply. The same applies to specimens shot on certain stretches of the Kafue Flats and Upper Zambesi. More remarkable is the fact that adults collected in Bangweulu Swamp carried their quota, though stones could not have been acquired anywhere in the neighbourhood. Several crocodiles shot near swamp villages in Bangweulu had also collected (in lieu of stones) pieces of broken glass and pottery—these could only have been deliberately swallowed. Again, Player tells me (8.2.56) that crocodiles examined by him in St. Lucia Estuary contained water-worn pebbles that

must have been gathered from the sea shore—in some cases this would have involved a journey of many miles.

Function of stones

It seems certain from the above evidence that stones are deliberately swallowed ; and, from their regular occurrence in stomachs of adult crocodiles, it is reasonable to suppose that they serve some physical or physiological function.

Various suggestions have been put forward : (1) that stones aid digestion, by the trituration of food ; (2) that they serve to relieve the pangs of hunger during periods of enforced starvation ; or (3) that they serve a hydrostatic function. These may be considered in order.

Digestive function

Hasselquist (1766) states : “ The crocodile swallows stones to assist digestion, after the manner of seed-eating birds, which commit to the stomach the work of mastication, as well as concoction, being destitute of the instruments adapted to that purpose.” Although this explanation has been reiterated by most authors who refer to the subject and has become the one commonly accepted, it is unsupported by evidence, and the following facts tell against it.

(a) The analogy with graminivorous birds is false, because the crocodile has no gizzard.

(b) In early life, before stomach stones have been acquired, crocodiles feed largely upon prey with hard chitinous or calcareous exoskeletons ; whereas adults, carrying stones, take more fleshy foods that require less trituration.

(c) Brittle structures such as the thin horny opercula of gastropods would be the first to be affected by gastric trituration ; yet these are commonly found unbroken in stomachs containing stones, long after the calcareous shells and fleshy parts of the snails have been digested. Nematodes remain alive and unaffected.

(d) Most carnivorous animals which swallow their prey whole, without mastication, such as predaceous fishes, and pelicans and many other fish-eating birds, digest their food without the aid of stones. In cormorants and darters the gastric juices are quite adequate to deal with armoured and spine-bearing fish such as *Clarias*, *Bagrus*, *Auchenoglanis* and *Synodontis*—often the very species which crocodiles are themselves taking.

(e) Examination of stomach contents of crocodiles reveals entire bones in all stages of digestion ; and there is no evidence that stones aid the process.

Filling function

In certain Pinnepedia, the second explanation seems to be the most satisfactory one. Thus Laws (1956) concluded from his study of their mode of occurrence in

the Elephant Seal, that stomach stones serve "to relieve 'hunger pangs,' by providing the stomach muscles with bulk, upon which they may contract," when the animals are fasting ashore.

But no such explanation could be valid for crocodiles, which, as in Uganda, inhabit permanent waters with a plentiful food supply, and which feed throughout the year. Nor is there any evidence that females contain more stones during the incubation period when they may be fasting, than at other times.

Hydrostatic function

The suggestion that stones serve as ballast in the crocodile which "requires the finest adjustment and poise in the water" was apparently first made by Brander (1925). Now that adequate data are available, his suggestion—then unsupported by evidence—warrants further consideration.

(a) The relation, already referred to, between body weight and the weight of stomach stones carried by adult crocodiles is itself suggestive of an explanation in terms of specific gravity of the swimming or submerged animal. If a crocodile carries a cargo amounting to one per cent. of its body weight, how will this affect its weight in the water? The information in Table 10 provides a partial answer to this question.

TABLE 10

Weight of the body on land, compared with weight when submerged.

Serial No.	Locality	Sex	Length	Body weight kg.		Submerged weight as percentage of body weight	Specific gravity
				on land	submerged		
400	Kafue	♂	1.005	2.45	0.190	7.76	1.084
399	Kafue	♀	1.060	2.97	0.210	7.12	1.077
380	Kafue	♂	1.210	4.80	0.340	7.08	1.076
388	Kafue	♀	1.230	4.95	0.375	7.58	1.082
379	Kafue	♀	1.290	6.30	0.490	7.78	1.084
573	Zambesi	♂	1.310	5.80	0.420	7.24	1.078
398	Kafue	♀	1.370	7.80	0.600	7.69	1.083
574	Zambesi	♂	1.860	19.50	1.400	7.18	1.077
At. 1	Luangwa	♀	2.320	44.00	3.200	7.27	1.078

The submerged weight, when expressed as a percentage of the weight on land, ranges in the nine specimens examined from 7.07 to 7.78 (mean 7.41); and the specific gravity from 1.076 to 1.084 (mean 1.080).

Assuming that the weight relationships are similar for large specimens (the series examined shows no apparent change in the ratio with growth) a standard (one per cent.) load of stones will account for about one-eighth of the crocodile's weight when submerged, and will raise the specific gravity from 1.08 to about 1.09. This loading effect will of course be proportionately greater for individuals

that have ingested more than the normal quota of stones : examples are given in Table 11.

TABLE 11

Serial No.	Locality	Sex	Crocodile		Stomach stones	
			Length in metres	Weight in kg.	Weight in gm.	Percent. weight
441	Mongu, Zambesi	♂	2.310	45.0	850	1.89
214	Olandi, Kalungwishi	♀	3.160	143.0	2700	1.89
446	Mongu, Zambesi	♀	1.560	11.5	225	1.96
416	Mongu, Zambesi	♀	3.040	106.5	2100	1.97
509	Mongu, Zambesi	♀	2.990	109.5	2160	1.97
210	Olandi, Kalungwishi	♀	3.840	239.0	5100	2.13
519	Mongu, Zambesi	♀	1.890	22.3	480	2.15
34	Fajao, Nile	♀	3.480	162.5	3675	2.26
345	Lochinvar, Kafue	♀	3.160	119.0	2700	2.27
460	Mongu, Zambesi	♀	2.250	42.5	970	2.28
313	Ndevu, Luangwa	♀	2.940	83.8	2050	2.45
136	Mutwamina, Bangweulu	♂	3.375	164.0	4540	2.77

For example, a 2.5 per cent cargo of stones will account for about one-quarter of the crocodile's submerged weight, and will raise the specific gravity to about 1.11.

(b) The biological value of ballast is likely to be two-fold. (1) It will enable the crocodile to lie submerged on the bottom (as commonly observed below Murchison Falls) in places where the strong current would tend to dislodge an animal of lower specific gravity. (ii) Crocodiles have need of extra effective weight when holding a large prey under water until it is drowned. When a large animal, such as a buffalo or waterbuck, has been captured, there follows a prolonged struggle during which the victim may several times regain the surface (as was seen below Paraa in 1956). Stomach ballast cannot fail to favour the predator in these circumstances.

(c) There is also evidence that stomach stones subserve further hydrostatic functions—acting (i) as an anterior counterpoise, and (ii) as a ventral stabilizing force. In this connexion, it is important to appreciate the position which the stones occupy in the body of the swimming animal. Firstly, the stomach lies anterior to the centre of gravity which is near the posterior end of the body. Secondly, X-ray photographs (Plate 5, figs. 1 and 2) of living crocodiles show that the stones lie low in the stomach and adjacent to the ventral body-wall. In this position they will lower the centre of gravity and act in a manner analogous to cargo in a ship's hold, making for stability in the swimming animal. This downward stabilizing force will be enhanced by the upward and lifting component from the more dorsal lungs.

The need for such a mechanism is demonstrated by the instability of stoneless young when placed in deep water. In nature, young crocodiles shun open water, even when feeding at night. Experiments have shown that they tend to be both

tail-heavy and top-heavy. They cannot lie level at the surface like their stone-carrying elders, and movements of the limbs are often necessary to counteract rolling. This is in marked contrast to the easy poise seen in the floating adult (Plate 4, fig. 1).

GROWTH AND AGE

Growth rate

Information hitherto available on the rate of growth under natural conditions is largely conjectural, and the assessments are highly conflicting. For example, Pitman (1931) estimated that in early life growth does not exceed one inch per annum. According to Brehm (1914) the rate is at first four inches per annum and in later life slower. In contrast, Siggins (1931) states that growth during the first few years is very fast and that at six years of age the crocodile will be as many feet in length.

Long-term field measurements of marked crocodiles of known age—comparable to those given by McIlhenny (1934) for the American alligator (see p. 255) are clearly needed; and it was with great interest that I learned of a specimen that had been measured, over a period of twenty-two years, by Mr E. Davison, Chief Game Warden, Southern Rhodesia. Davison (25.2.58) has most kindly sent me details, and permission to publish his observations.

The specimen was hatched on the Shangani R. in December 1935 and has been under observation in natural conditions. For the first nineteen months it was kept in a large pond, where it fed on grasshoppers, crickets, moths and other insects. It was seen to catch a bird when eighteen months old. In July 1937 it was transferred to a natural pan and in 1939 to a larger pan, containing *Clarias*. This and another pan to which it wanders in the wet season, are used by a large variety of game—from baby warthogs to elephant. The crocodile is known to have killed a wild cat and a full-grown warthog, and it has frequently been seen to catch fish and birds, including doves, duck, pelicans and plovers: during the rains toads are also taken.

Measurements, in inches, recorded by Davison are as follows:

Dec. 1935 c. 11	Aug. 1937 26.5	Dec. 1945 88
June 1936 12	Dec. 1937 30	Dec. 1946 90
Aug. 1936 16	Oct. 1938 44	Dec. 1949 93
Nov. 1936 22	Dec. 1941 72	Nov. 1957 104
Mar. 1937 26.5	Dec. 1942 84			

Growth of this crocodile is plotted in Fig. 13.

Flower (1933) gives details for four specimens of *C. niloticus* in the Giza Zoological Gardens, Cairo, where the animals were kept under fairly natural conditions of climate and environment. Bigalke (1929) records the length of a specimen from Pretoria, known to be twenty-two years old. Dr L. Harrison Matthews (20.3.57) has sent me further measurements of two specimens of known age now living in the Reptile House, Regent's Park. The relevant data for these and some other crocodiles are listed (p. 246), in order of age, and plotted for comparison with Davison's measurements in Fig. 13.

Cambridge	6 weeks	0.312 m. (12.3 ins.)	—
Cambridge	1 year	0.530 m. (20.8 ins.)	0.39 kg.
London	1 year, 7 months	0.594 m. (23.5 ins.)	0.45 kg.
Cairo	1 year, 8 months	0.705 m. (28 ins.)	1.8 kg.
Cambridge	2 years, 10 months	0.993 m. (39 ins.)	3.3 kg.
Cairo	4 years	1.657 m. (65 ins.)	18.0 kg.
London	4 years, 4 months	1.850 m. (73 ins.)	—
Cairo	4 years, 6 months	1.840 m. (72 ins.)	30.0 kg.
Cairo	8 years	2.340 m. (92 ins.)	72.5 kg.
London	12 years, 9 months	2.400 m. (94 ins.)	—
Pretoria	22 years	2.850 m. (112 ins.)	—

It will be seen that the growth rates for the free living and captive specimens are generally similar up to the age of twenty-two years, when the recorded lengths are 104 and 112 inches respectively. In Davison's crocodile growth is rapid during the first seven years, the mean annual increment being 10.4 inches (or 265 mm.). Thereafter the growth-rate is slower and remarkably steady over a period of fifteen years, during which the animal gained only a further 20 inches in length, with a mean increase of 1.4 inches (or 36 mm.) per annum. The corresponding mean annual increments shown in captive specimens are : for the first seven years, about 11 inches (or 280 mm.) ; for the next fifteen years, about 1.5 inches (or 40 mm.).

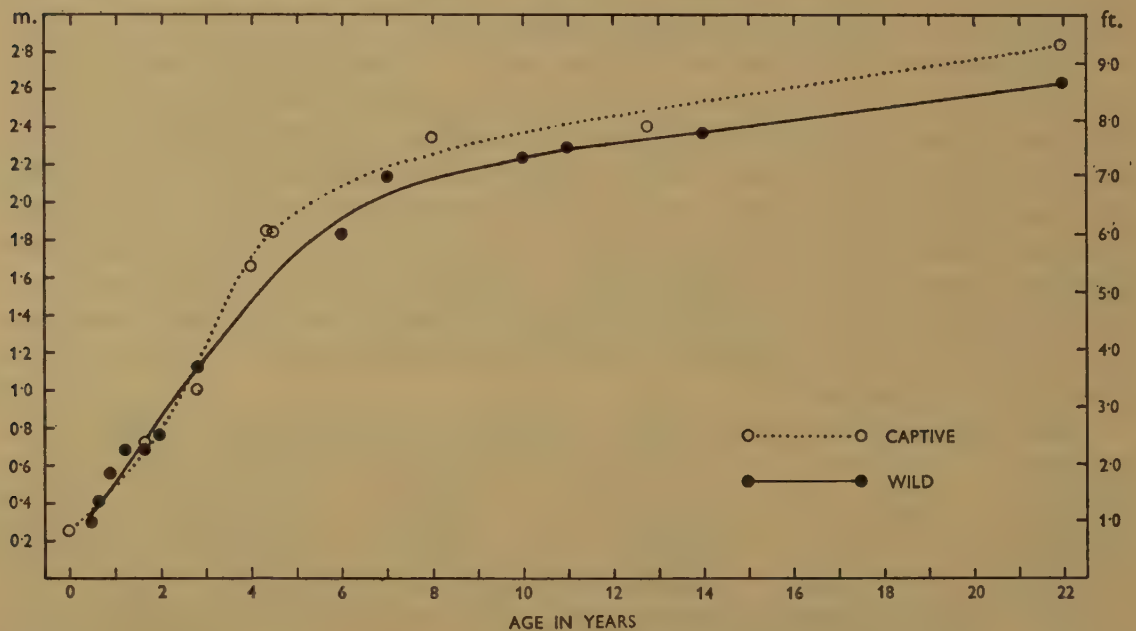


Fig. 13. Growth rate of *C. niloticus*, based upon observations of specimens in captivity and upon a free-living specimen (Davison's data).

The length of crocodiles examined from the Luangwa, Lunsemfwa, Kafue and Zambesi rivers, plotted against dates of capture, is shown in the scatter diagram, Fig. 14 : (males, black ; females, white ; sex unrecorded (records by Voigt), black and white circles). Although these measurements come from an area where there is a well-marked breeding season, the length frequency distribution defies

interpretation in terms of growth and age beyond the third year of life, since evidently the variation in length within respective year groups is large in comparison with the mean yearly increments. The superimposed year groups (shown in dotted lines) are based on Davison's data.

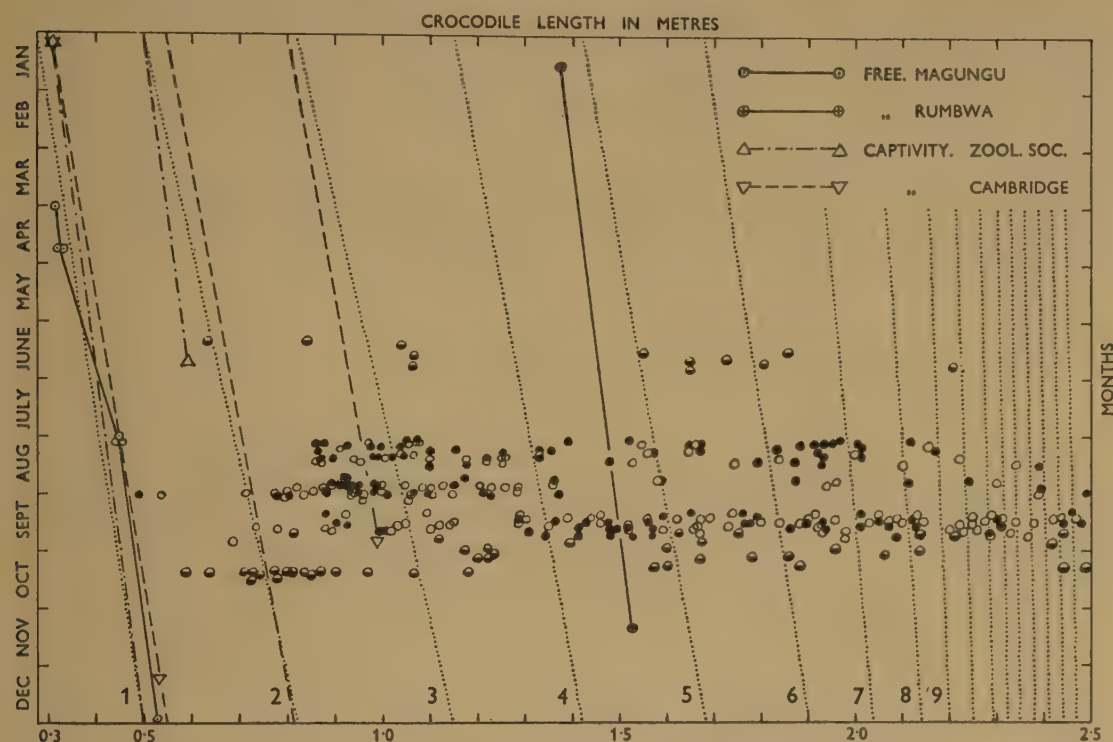


Fig. 14. Growth rate of *C. niloticus*. The scatter diagram shows the total length and date of capture of crocodiles examined from Luangwa Valley, Kafue Flats, and Upper Zambesi; males—black; females—white; sex unknown—black and white circles. The dotted lines, indicating year groups, are based on Davison's data. The continuous and broken lines show growth rates based on measurements in the field and in captivity respectively.

Also plotted in this figure are various growth data for young specimens measured in captivity and in the wild state. (a) The former are based on a series of newly-hatched young captured on Buvu Island and reared in Cambridge and the Society's Gardens. (b) Comparative data of growth during the first year of life in the wild state are provided by specimens caught in the meres near Magungu, Victoria Nile (see Table 12).

TABLE 12

No.	Authority	Date	Age	Length in mm.	Weight in gm.
S.2	J.S.	31.3.57	newly-hatched	315	—
S.3	J.S.	23.4.57	3 weeks	320	—
S.4	J.S.	24.4.57	3 weeks	325	—
106	H.B.C.	1.8.56	4 months	450	140
107	H.B.C.	3.8.56	4 months	455	c. 150
108	H.B.C.	3.8.56	4 months	447	c. 150
222	H.B.C.	29.12.56	9 months	530	250

For the records made in March and April 1957, I am indebted to Mr John Savidge. The hatching date of all specimens listed is taken to be about the end of March.

Two further records, of larger crocodiles of unknown age, relate to specimens shot in the remote islet of Rumbwa, Sese, as follows : No. 2, 16.1.52, length 1.375 m., weight 7.0 kg.; No. 101, 10.11.52, length 1.525 m., weight 10.75 kg. The increase in length of 150 mm. (about 6 ins.), over a period of 10 months, shown by these measurements agrees well with the known growth-rate of crocodiles of comparable size, and it is probably that the two specimens were hatched in the same season and perhaps from the same clutch.

It will be seen on reference to Fig. 14 that the growth rates recorded for these various specimens conform closely to the gradients derived from Davison's measurements.

Size attained

It is not easy to assess the validity of records of very large crocodiles that have been reported from various parts of Africa. Visual estimates of length, like those of Brue (25 ft.) and Barbot (30 ft.) cited by Cuvier (1831) are always unreliable ; and the only valid information is that provided by measurements, with steel-tape or otherwise, of the distance between pegs set at the snout and tail-tip.

The question of the maximum length attained by *C. niloticus* is never likely to be satisfactorily settled. Some herpetologists have undoubtedly erred in understatement. Thus Ditmars (1922) accepts 16 feet as the maximum. In their recent works, Pope (1957) and Schmidt & Inger (1957) repeat this figure—which is far below measurements reliably reported.

Against the scepticism with which older records are to be regarded, must be set the fact that crocodiles require a long time, perhaps at least 100 years, to attain spectacular size : under modern conditions, veterans have little chance of survival, and have already vanished from most African waters.

Nor are the verified measurements of specimens in museums a reliable criterion. On the rare occasions when exceptionally large individuals have been killed, it is almost inevitable that they should be lost to science as specimens. But the absence of such material cannot be accepted as sufficient reason for rejecting evidence from the field.

The following records provide some indication of the maximum length attained by *C. niloticus* in Central and South Africa.

Central Africa.—Exceptionally large crocodiles do not appear to have been encountered recently in the Rhodesias. L. E. Vaughan (Senior Game Ranger) reports that the largest actually measured by him in Northern Rhodesia was 16 feet 7 inches. He states that he has measured several over 16 feet in length ; but that the average large crocodile in the Kafue appears to be in the 13 to 15 feet range. A photograph of a 16-foot crocodile shot in the Kafue by Clyde Sussens was published in the *N.R. Journal* (1955) : its weight was stated to be between

1,500 and 1,600 lbs. In former years, Hubbard (1927) shot a specimen in the Kafue which, measured by steel-tape, was "just a fraction larger than seventeen feet five inches."

From Nyasaland, Loveridge (1953) reports a specimen shot by C. C. Yiannakis, near Chipoko, that was said to measure 18 feet 10 inches.

East Africa.—A number of very large specimens have been reliably reported from Uganda, where the species appears to reach its greatest size in the Lower Semliki and the Murchison reach of the Victoria Nile. At Fajao, Murchison Falls, Hobley (1921) shot a crocodile in 1900 of which he writes: "The only authentic measurement . . . that I can vouch for was one of my own, it was 18 feet from tip of snout to tip of tail, measured between perpendiculars." Two males, killed and measured on the Semliki by a Game Ranger in 1950, were 16 feet 10 inches and 18 feet 2 inches in length (Kinloch, 1951). In 1952, the Marketing Corporation which employed hunters on the Lower Semliki received a skin which measured 19 feet 6 inches. Mr E. V. Hippel, an experienced professional hunter, tells me (29.10.54) that during a penetrating safari in the Lower Semliki in June, 1954, he shot his largest crocodile—a female which measured 18 feet 4 inches. If the sex has been correctly reported, it must stand as a record; this crocodile exceeds by over three feet the maximum length reported by Pitman for a female in Lake Victoria, and is in fact slightly larger than Pitman's largest male—an 18-foot specimen shot in 1942.

Mr Douglas Jones informed me that crocodiles of exceptional size were formerly found in the Juba River: one which he measured at Bardera was just over 21 feet. The largest recorded by Mr Bousfield (Swynnerton, unpub. report) from Lake Rukwa was 17 feet 4½ inches. In Lake Victoria the biggest crocodiles have been reported from the Emin Pasha Gulf area. In 1905 the Duke of Mecklenberg killed one near Mwanza which was said to measure 6·5 metres, or nearly 21 feet 6 inches (Hubbard, 1927). Mr J. D. Kelsall (L.V. Fisheries Service) has sent me (25.10.53) the following information supplied by a professional hunter named Erich Nowotny. He states that the only really big crocodile he could personally vouch for was one he shot about a mile west of Nungwe, Emin Pasha Gulf, in 1949, which measured exactly 21 feet, and at a rough estimate weighed about a ton. When hunting one night near Senga Point at the N.E. entrance to Nungwe Bay, in 1948, Nowotny drew alongside a crocodile that was apparently asleep on the water: he states that this specimen was "appreciably longer than the 20-foot canoe" and he estimated its length at not less than 22 feet. Nowotny also told Kelsall that in 1950 an Indian, trapping crocodiles in the Butundwi Bay area, offered him twenty-seven skins for sale: only two were under 18 feet in length—allowing for the fact that these were measurements of skins, he estimated that the crocodiles in this batch must have averaged about 19 feet in length. In the late forties, according to the same hunter, crocodiles of 20 to 22 feet were quite commonly taken in the Gulf by natives using hooks.

In some waters, the Nile Crocodile never attains a large size. For example, the largest of over 1,000 shot by Nowotny in Malagarasi Swamp was only 12 feet

in length. Hippel tells me that the largest he obtained in Lake Kioga measured only 12 feet 6 inches ; and 90 per cent. of 500 collected by him in 1944 were from 7 to 10 feet long (Pitman, 1948). Again, according to Hobley (1919), crocodiles in Lake Baringo rarely exceed 9 feet. More remarkable, in this connexion, are the so-called "pigmy crocodiles" of the Aswa River in Northern Uganda (Pitman, 1931, 1934 ; Salmon, 1933), measuring between 5 and 6 feet.

Thus it is evident that the maximum size attained differs widely according to locality. Where conditions for maximum growth are favourable, there seems to be reliable evidence that the species may reach a length of at least 20 feet ; while some records of even larger crocodiles appear to be valid.

Longevity

The potential length of life in the Nile Crocodile is not known. Some light is thrown upon the subject by authentic life-records of animals kept in captivity. But as criteria such records are far from satisfactory. It is often impossible to verify the dates when specimens, reputed to have lived to a great age, were first received into captivity. And it is probable that crocodiles live longer in the wild state than in the restricted and artificial conditions that obtain in a reptile house : as Flower (1937) has remarked—"in general . . . reptiles do not *live* in captivity, but pine away."

Yet from records which Flower (1925, 1937) accepted as absolutely authentic, it is clear that crocodilians are long lived. The ages, in years, attained by the oldest-known individuals of various species, as given by Flower, are as follows :

<i>Gavialis gangeticus</i> (Indian Gharial)	London	24
<i>Tomistoma schlegelii</i> (Malay Gharial)	New York	23
<i>Osteolaemus tetraspis</i> (Broad-fronted Crocodile)	Frankfurt	24
<i>Crocodilus niloticus</i> (Nile Crocodile)	Berlin	25
<i>Crocodilus cataphractus</i> (Long-nosed Crocodile)	Amsterdam	20
<i>Crocodilus palustris</i> (Mugger)	Trivandrum	31
<i>Crocodilus porosus</i> (Estuarine Crocodile)	? Frankfurt	21
<i>Crocodilus siamensis</i> (Siamese Crocodile)	London	16
<i>Crocodilus intermedius</i> (Orinoco Crocodile)	Amsterdam	23
<i>Alligator sinensis</i> (Chinese Alligator)	Berlin	50
<i>Alligator mississippiensis</i> (American Alligator)	Dresden	56
<i>Caiman niger</i> (Black Cayman)	Munster	28, 130

Dr H. G. Vevers tells me (1.12.59) that a Gharial which died in the Reptile House in 1941 had lived in the Gardens for 28 years 9 months. Fullest information is available for the American alligator. In his summary Flower writes : "We know of twenty individual Mississippi alligators that show an average life of thirty-three years and two-and-a-half months. No fewer than eleven out of these twenty individuals being still alive at the time when these notes were made, proves that the average duration of life will be longer still. Five of these twenty reached an age of forty or more years. . . . The oldest known . . . is the still living veteran of Dresden of 56 years."

Such evidence from zoological gardens, taken together with what is known (a) of the growth-curve in free-living and captive specimens of *C. niloticus*, and

(b) of the length attained by this species in nature, undoubtedly points to a very long potential life-span. If growth after 22 years continues at the rate indicated by Davison's field measurements, at about 1.4 inches per annum, then a crocodile measuring 15 feet in length would be about 76 years old, and one measuring 18 feet would be over 100 years old. But if, as is most likely, the growth curve flattens out in late life, then the largest known specimens must have survived well into their second century.

SIZE AND SEX RATIO

The sexes of 651 crocodiles of known length have been recorded during the present investigation, and the data available throw some light upon the changing constitution of the population as it ages. The relevant data are given, under 0.25 metre length groups, in Table 13.

TABLE 13
Number and percentage of the sexes, by length groups.

<i>Crocodile length in metres</i>	<i>Size of sample</i>	<i>Number</i>		<i>Per cent.</i>	
		<i>males</i>	<i>females</i>	<i>males</i>	<i>females</i>
0.25—0.50	3	3	0	—	—
0.50—0.75	9	5	4	55.6	44.4
0.75—1.00	93	47	46	50.5	49.5
1.00—1.25	74	36	38	48.6	51.4
1.25—1.50	47	24	23	51.1	48.9
1.50—1.75	46	20	26	43.5	56.5
1.75—2.00	41	24	17	58.5	41.5
2.00—2.25	46	20	26	43.5	56.5
2.25—2.50	52	24	28	46.2	53.8
2.50—2.75	51	22	29	43.1	56.9
2.75—3.00	59	22	37	37.3	62.7
3.00—3.25	59	17	42	28.8	72.1
3.25—3.50	29	18	11	62.1	37.9
3.50—3.75	19	19	0	100.0	0.0
3.75—4.00	11	11	0	100.0	0.0
4.00—4.25	4	4	0	100.0	0.0
4.25—4.50	5	5	0	100.0	0.0
4.50—4.75	3	3	0	100.0	0.0

For the series as a whole, sexes are almost equal in number, there being 324 males and 327 females. This equality is also seen among crocodiles of the smaller length groups. Thus, 226 specimens measuring less than 1.50 metres occur in the proportion of 115 males and 111 females; and 185 specimens measuring between 1.5 and 2.5 metres, in the proportion of eighty-eight males and ninety-seven females. For the 411 specimens below 2.5 metres, the ratio is 49.4 and 50.6 respectively.

Above this length, the proportions of the sexes diverge and in successive length groups show the following trends. At first there is a fall in the percentage of males, until in the 3.0 to 3.25 metre group, containing fifty-nine specimens, only seventeen (or 28.8 per cent.) are males. Thereafter the trend is steeply reversed. Of seventy-one specimens above 3.25 metres, only eleven (or 15.5 per cent.) are

females, and all these fall within the 3.25 to 3.5 metre group. These changing ratios are shown graphically in Fig. 15. They are explained by the fact that the males (whether by faster growth or by longer-continued growth, see p. 255) attain a greater length than the females. The disparity in adult size is expressed graphically in Fig. 16, which shows the length frequency distributions for each sex.

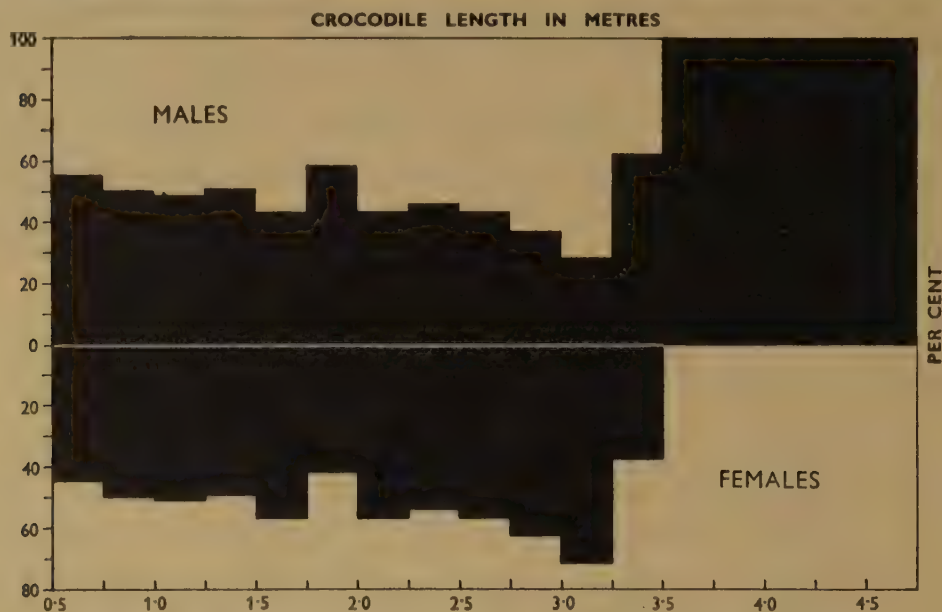


Fig. 15. Histogram showing sex ratio in relation to crocodile length.

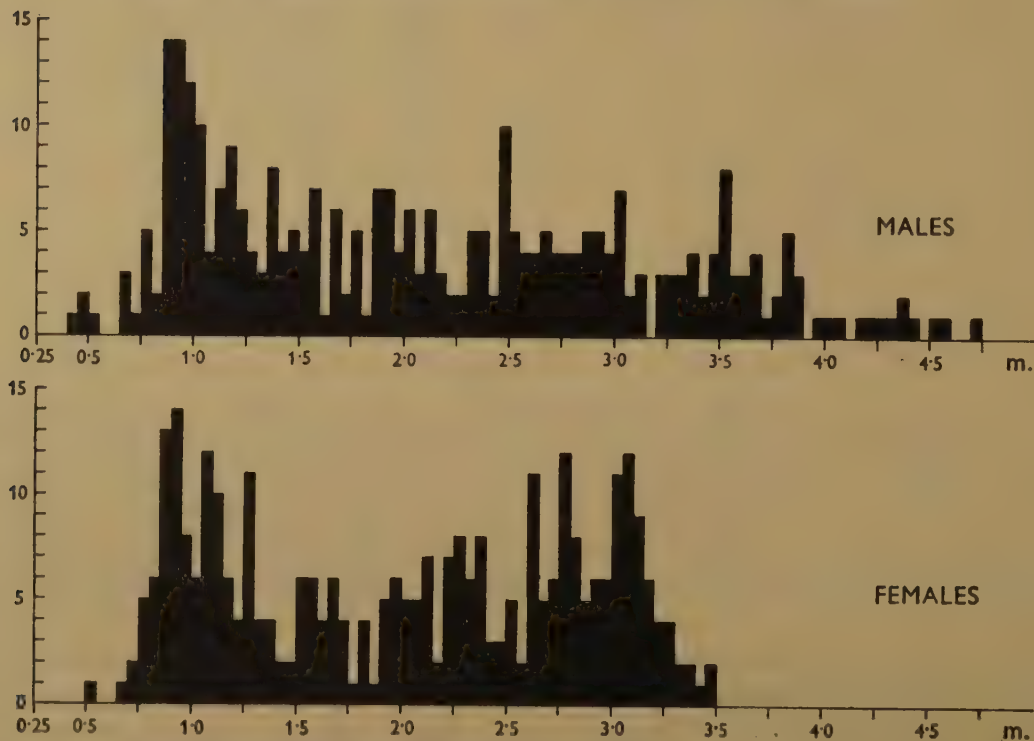


Fig. 16. Length frequency distribution, by sexes, of 651 crocodiles (324 males, 327 females) examined in Uganda and Northern Rhodesia (1952, 1956 and 1957).

PART II. BREEDING BIOLOGY

BREEDING MATURITY

The male

The breeding condition is easily recognizable in the field, by inspection of the gonads. In the immature crocodile the testis is relatively small in size, granular in texture, attenuated in shape, and liver coloured. In the breeding male the organ becomes greatly enlarged and distended, its texture is smooth and its colour bluish-white. Measurements of the testis in crocodiles of different sizes are given in Table 14. It will be seen that its relative weight is nearly twenty times greater in the sexually functional male (No. 340) than in the juvenile or non-breeding males.

TABLE 14
Measurements and weight of the testis.

Serial No.	Locality	Crocodile		Testis		Testis wt. $\times 100$
		Length in m.	Weight in kg.	measurements in mm.	weight in g.	Body wt.
130	Bangweula	1.350	7.26	30 \times 8 \times 5	0.6	0.0083
133	Bangweula	2.010	27.7	38 \times 11 \times 3	1.4	0.0051
95	Victoria Nile	2.200	39.5	43 \times 17 \times 9	3.5	0.0089
121	Bangweulu	2.340	46.3	73 \times 10 \times 8	3.9	0.0084
124	Bangweulu	2.550	76.7	73 \times 21 \times 13	11.8	0.0154
12	Semilik R.	2.750	67.0	65 \times 15 \times 9	4.7	0.0070
125	Bangweulu	3.000	100.7	90 \times 18 \times 12	c.10.0	c.0.0099
340	Kafue Flats	4.400	414.5	200 \times 88 \times 50	575.0	0.1387

Among 110 males of all sizes examined from the Kafue and Upper Zambesi during the breeding season of 1957, the smallest animals with testes enlarged and active measured 3.33 and 3.09 metres respectively. Measurements of crocodiles from the Luangwa and Lunsemfwa rivers are likely to be misleading since in these waters professional hunters had already drastically reduced the breeding population. Of fifty-five males examined in the Luangwa Valley, none attained 3 metres in length; and here the smallest sexually mature male measured 2.80 metres. Complete data are not available for the series of males obtained in the Northern Province, 1956. However, Dr A. J. Marshall (4.6.57) has very kindly prepared and examined sections of testes from Bangweulu Swamp. Crocodile No. 124, measuring 2.55 metres, was the most advanced specimen submitted to him for examination: this showed proliferation of germ cells and a well-organised functional lipoidal interstitium, but the animal had not reached a size at which successful male activity could occur.

From information at present available, it would appear that sexual maturity is normally reached by the male at a length of about 2.9 to 3.3 metres: the weight of such animals is between about 80 and 160 kg.

The female

Breeding females were recognised on the following basis: (a) those ovulating,

with ova ranging from about 2 mm. in diameter upwards ; (b) those with oviduct eggs, unshelled or shelled ; and (c) spent females, in which the ovaries, undergoing resorption, are flaccid, granular and discoloured, and the oviducts still much distended and with prominent vasularization.

Data are available for all females from Bangweulu Swamp, Mweru Wa Ntipa and the Kalungwishi River in the Northern Province, and from Luangwa, Kafue and Zambesi Rivers. In the three northern localities the smallest measurements for breeding females are 2.38, 2.51 and 3.02 metres respectively ; and from the southern localities 2.59, 2.70 and 2.82 metres respectively. The weight of such animals is between about 60 and 120 kg. But these are minimum sizes : about half the females are breeding at about 3 metres length and 120 kg. weight.

Pitman's measurements of nesting crocodiles provide further valuable information on the size-range of breeding females, and, in the present context, on the length at which sexual maturity is reached. In view of the crocodile's decline in recent years, it is virtually certain that such extensive observations will never be repeated, and I am most grateful for him for permission to place on record the following analysis of measurements recorded in his unpublished notes.

Fig. 17 shows the length frequency distribution of 855 females shot on the breeding grounds and known to have nests, during the years 1940 to 1949. The largest numbers of breeding females occur in the length ranges between 9 feet

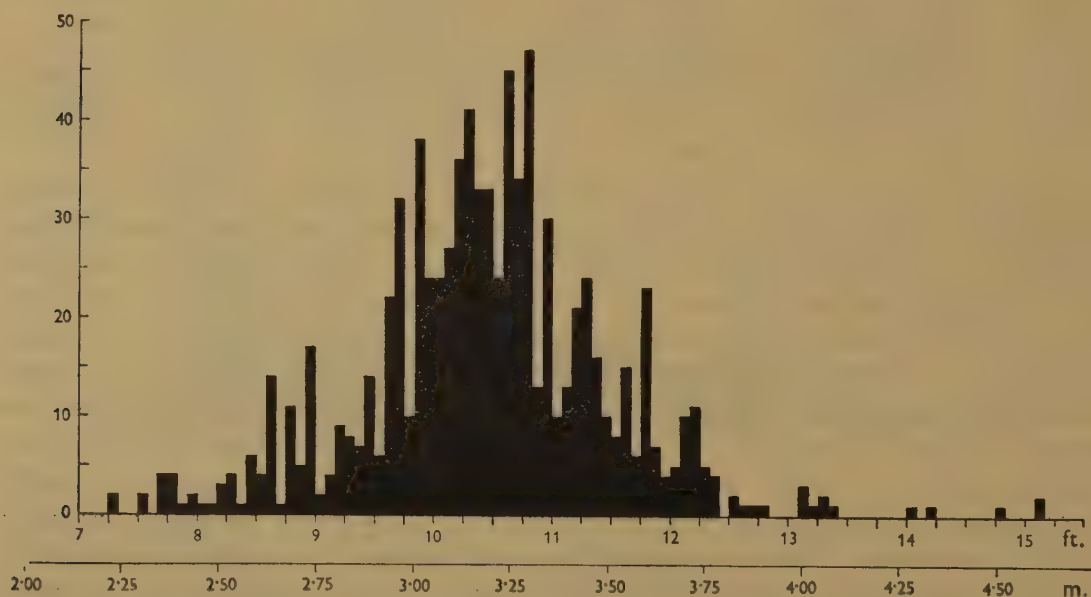


Fig. 17. Histogram showing the length frequency distribution of 855 breeding females shot at the nest in northern Lake Victoria. (Pitman's unpublished notes.)

6 inches and 11 feet 6 inches ; and the mean length is 10 feet 5 inches. Specimens within the size range between 8 feet 6 inches and 12 feet 6 inches comprise 807 (or 94.4 per cent.) of the total.

Very few females (less than 2 per cent.) were nesting before they had attained a length of 8 feet (2.44 m.). The smallest among this large sample are as follows :

four, 7 feet 8 inches ; two, 7 feet 6 inches ; and two, 7 feet 3 inches ; all from the Sese Islands. Pitman (19.1.56) further confirms that over a period of some fifteen years, during which he and his Fish Guards measured between 1,500 and 2,000 females, 7 feet 2 inches (or 2.19 m.) was the smallest size recorded on the breeding grounds.

The sexes compared

Comparative data for breeding crocodiles, of both sexes, from Northern Rhodesia, are given in Tables 15 and 16. Fig. 18 shows the percentage of males and females that were in breeding condition, by length groups. Length and weight of breeding

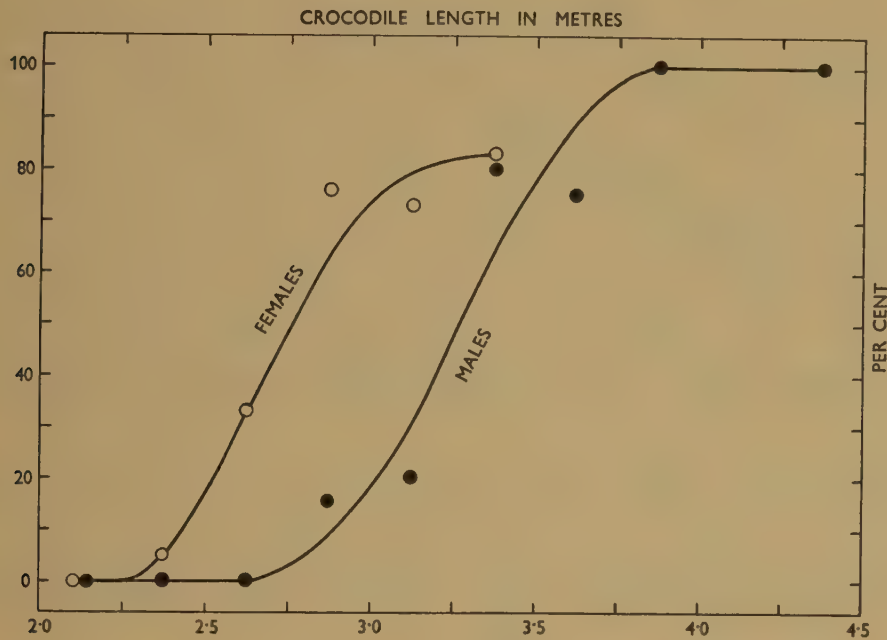


Fig. 18. Smoothed curves, showing the percentage of males and females breeding, in relation to crocodile length.

specimens of both sexes, from the southern localities, are plotted in Fig. 19. It will be seen that for crocodiles of comparable length, the females are considerably heavier than the males, but that the females become sexually mature at a considerably shorter length than the males.

If the rate of growth is the same for both sexes, the females must mature at an earlier age than the males. On the other hand, if the sexes attain maturity at about the same age, growth in the male must be more rapid. From what is known of growth in the American alligator the disparity is almost certainly due to differential growth rate.

Working in the Wild Life Refuge on Avery Island, Louisiana, McIlhenny (1934) toe-marked thirty-eight alligators in 1921 and kept them under observation for

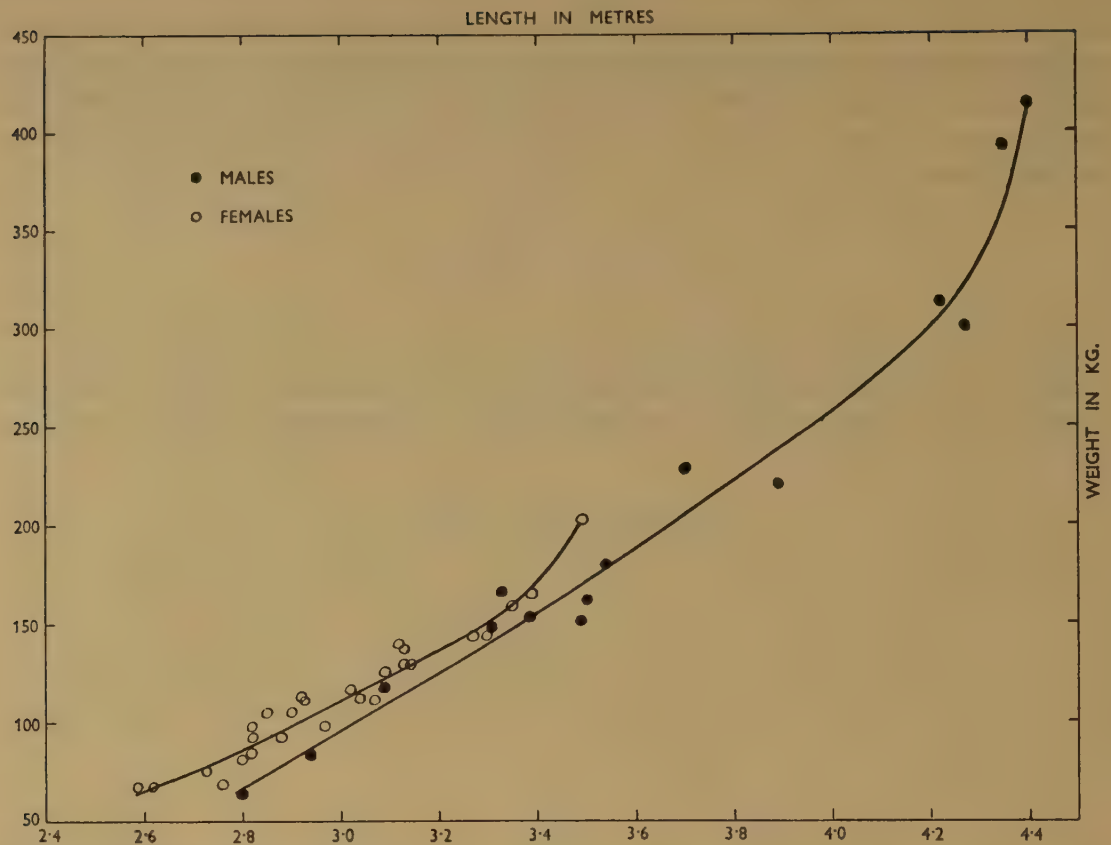


Fig. 19. The relation of length to weight in breeding crocodiles, of both sexes, from Luangwa Valley, Kafue Flats and Upper Zambesi (to which one record from Magungu is added).

eleven years. His protracted observations are of great interest, for they give the only available accurate picture of growth, in the wild state, of specimens whose ages are known. His records reveal a growth differential between the sexes; and indicate the size and age at which the female attains sexual maturity.

TABLE 15

Number and percentage of crocodiles in breeding condition, by length groups. Males—records from Luangwa, Kafue and Upper Zambesi; females—in addition, records from Bangweulu and Mweru.

<i>Length group metres</i>	<i>Males</i>			<i>Females</i>		
	<i>No. not breeding</i>	<i>No. breeding</i>	<i>Per cent. breeding</i>	<i>No. not breeding</i>	<i>No. breeding</i>	<i>Per cent. breeding</i>
2.00-2.25	12	0	0.0	18	0	0.0
2.25-2.50	10	0	0.0	20	1	4.8
2.50-2.75	12	0	0.0	12	6	33.3
2.75-3.00	11	2	15.4	6	19	76.0
3.00-3.25	4	1	20.0	7	19	73.1
3.25-3.50	1	4	80.0	1	5	83.3
3.50-3.75	1	3	75.0	—	—	—
3.75-4.00	0	1	100.0	—	—	—
4.00-4.25	—	—	—	—	—	—
4.25-4.50	0	3	100.0	—	—	—

TABLE 16

Length and weight of male and female crocodiles in breeding condition.

Locality	Size of Sample	Length, in m.			Weight, in kg.		
		Max.	Mean	Min.	Max.	Mean	Min.
<i>Males</i>							
Luangwa Valley	2	2.940	2.870	2.800	83.7	73.3	63.0
Kafue Flats	6	4.400	3.932	3.330	414.5	280.0	166.5
Upper Zambesi	6	3.890	3.445	3.090	221.7	159.0	118.0
<i>Females</i>							
Bangweulu Swamp	5	3.140	2.840	2.380	?	—	52.2
Mweru & Kalungwishi	17	3.180	2.951	2.510	143.0	103.4	65.8
Luangwa Valley	4	2.760	2.675	2.590	75.2	70.0	67.5
Kafue Flats	10	3.390	3.075	2.700	165.0	126.3	81.5
Upper Zambesi	14	3.490	3.014	2.820	201.7	117.0	84.0

Data given by McIlhenny are plotted as a graph in Fig. 20. (a) It will be seen that growth is most rapid in early life. Animals of both sexes show an average increase of about a foot per annum up to the fifth year. This rate of increase is continued by the males until about the seventh year, but after the fifth year the females grow more slowly. The rate becomes progressively slower in both sexes with increasing age. (b) Measurements of specimens killed and sexed between 1927 and 1932 clearly show the disparity in size (amounting to about 1 foot 9 inches in the tenth year) between males and females of corresponding ages.

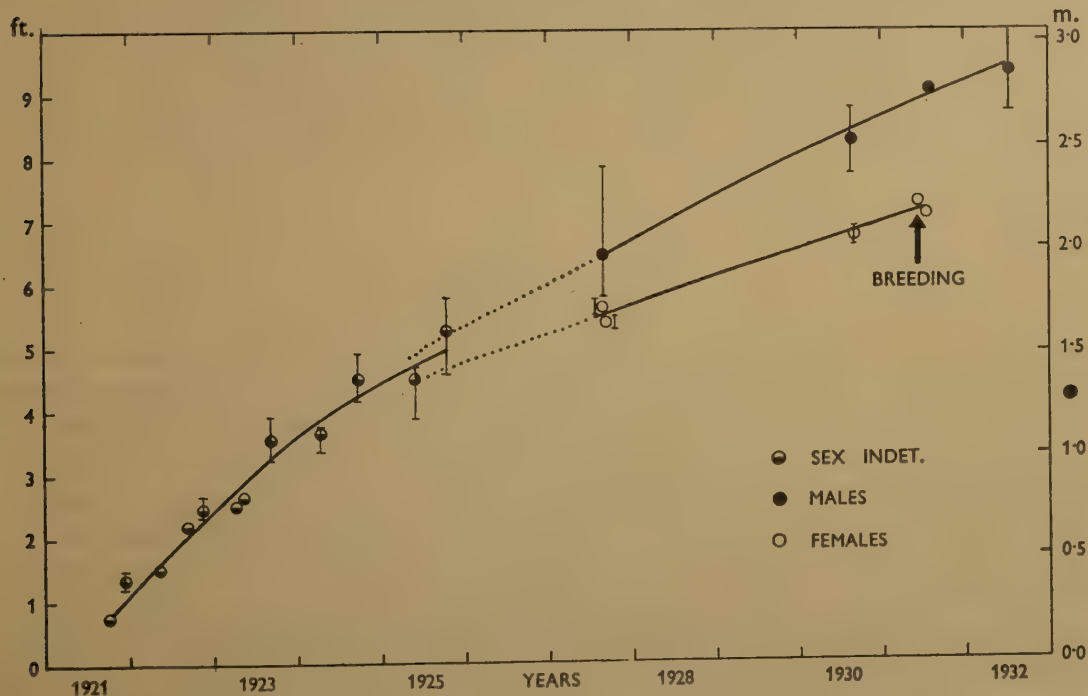


Fig. 20. Growth rate and breeding maturity in *Alligator mississippiensis* (based upon McIlhenny's observations from Avery Island, Louisiana).

At six years of age the divergence is already well marked. The starting age of this growth differential is not known, but reference to the graphs suggests that divergence may begin as early as in the fourth year of life. (c) The first of the marked females to breed began to nest at the age of nine years ten months, when 7 feet 3 inches in length and 116½ lbs. in weight.

Finally, as regards the age at which sexual maturity is attained : growth in *C. niloticus* is slower than in *A. mississippiensis*; but the recorded minimum length for a breeding female is the same for both species. Thus the female crocodile certainly does not reach maturity before ten years. Assuming that Davison's data represent the growth curve for a female, the age at minimum breeding length—the mean minimum for five localities (Table 16) is 2·60 metres (or 8 feet 6 inches)—would be about nineteen years. But only about half are breeding (see Fig. 18) at the length of 2·75 metres. If Davison's growth curve is that of a male, the time required for a female to attain maturity would be proportionally longer. The age of the average breeding stock will of course be much greater. Apart from mere academic interest, these conclusions have an important bearing upon the problem of crocodile conservation (see p. 327).

THE BREEDING SEASON

The breeding season, here defined as the season between laying and hatching of the eggs, was determined (a) by examination of the gonads in the female ; and (b) from the condition of embryos in nest-eggs. By either method it was often possible to determine, within a day or two, the date when eggs were about to be, or had been laid, i.e. as indicated by the presence of fully-shelled eggs in the oviducts or of newly-laid eggs in the nest. In other cases, the laying date could be estimated, more or less accurately, from the developmental stage of embryos.

Dates and localities

Tables 17 and 18 contain the relevant data, including estimated laying dates, for twenty-seven clutches in Uganda and twenty-five clutches in Northern Rhodesia and Barotseland. In all localities other than Lake Victoria there is a single, and apparently fairly well-defined breeding season. In the Upper Victoria Nile and Lake Kioga eggs were laid during the last three weeks of December ; in Lake Albert and the Victoria Nile below Murchison, in late December and the first week of January ; in Bangweulu Swamp, during the last week of August and the first half of September ; and in Mweru Wa Ntipa, the Kalungwishi, Kafue, Luangwa and Upper Zambesi Rivers, during the first three weeks of September. In northern Lake Victoria the situation is anomalous, in that fresh eggs may be found during two periods of the year—in August and early September, and again in December and January.

TABLE 17

Breeding dates : Uganda.

<i>Locality</i>	<i>Clutch Ser. No.</i>	<i>Date found</i>	<i>Condition</i>	<i>Estimated laying date</i>
L. Victoria : Nasu Point ..	Ug. 1	11. 1.52	c. 5 days	6. 1.52
Victoria Nile : Namasagale	Ug. a	13. 1.52	c. two weeks	30.12.52
„ Namasagale	Ug. b	13. 1.52	c. four weeks	16.12.52
„ Namasagale	Ug. c	13. 1.52	c. five weeks	9.12.52
Lake Victoria : Simu ..	Ug. 2	26. 2.52	c. five weeks	22. 1.52
„ Simu ..	Ug. 3	26. 2.52	near hatching	11.12.51
„ Mu ..	Ug. 4	28. 2.52	c. ten weeks	20.12.51
L. Kioga : Kigi ..	Ug. 5	4. 3.52	c. ten weeks	24.12.51
„ Kigi ..	Ug. 6	4. 3.52	c. ten weeks	24.12.51
„ Kigi ..	Ug. 7	4. 3.52	hatched 5-10.3.52	10.12.51
L. Victoria : Dagusi ..	Ug. 8	14. 8.52	c. 5 days	9. 8.52
„ Buvuma ..	Ug. 9	16. 8.52	new laid	15. 8.52
„ Buvuma ..	Ug. 10	30. 8.52	c. 4 days	26. 8.52
„ Bulago ..	Ug. 11	2. 9.52	new laid	1. 9.52
„ Bulago ..	Ug. 12	2. 9.52	c. 3 days	30. 8.52
„ Bulago ..	Ug. 13	2. 9.52	new laid	1. 9.52
„ Masovwe ..	Ug. 14	5. 9.52	c. two weeks	22. 8.52
„ Mbazi ..	Ug. 15	5. 9.52	new laid	4. 9.52
„ Buvu ..	Ug. 16	8. 9.52	c. ten weeks	30. 8.52
„ Buvu ..	Ug. 17	8. 9.52	hatched 10-22.11.52	24. 8.52
Albert Nile : Buligi ..	Ug. 18	23.12.56	new laid	22.12.56
Victoria Nile : Fajao ..	Ug. 19	2. 1.57	new laid	2. 1.57
„ Fajao ..	Ug. 20	5. 1.57	new laid	4. 1.57
„ Fajao ..	Ug. 21	5. 1.57	c. 36 hours	3. 1.57
„ Fajao ..	Ug. 22	5. 1.57	c. 10 days	26.12.56
„ Fajao ..	Ug. 23	5. 1.57	c. 36 hours	3. 1.57
„ Fajao ..	Ug. 24	7. 1.57	new laid	6. 1.57

While it is not suggested that the breeding season is confined within the narrow limits shown by the above observations, the dates are supported by information given me from the same localities by other observers. Thus, in Uganda, Wajalubi found crocodiles laying in the Semliki valley in December and hatching in March. Miss R. H. Lowe found crocodiles hatching at the end of March at Buhuka, Lake Albert, and in Lake Victoria Pitman (1936) reports laying in early August and hatching in late October and early November.

The following additional information is available from Northern Rhodesia. In the Luapula River and Bangweulu Swamp Holloway found newly-hatched young between 6th and 26th November during several seasons prior to 1952. According to the village headman at Kansenga (Bangweulu) crocodiles hatch in November in Lake Chali. Ansell (1.10.58) records a clutch new-laid on 11th September from the Luombwa River ; and (in litt. 8.12.59) a clutch ready to hatch in mid-November in the Kabompo District. From the Kafue, Poles (1956) found shelled oviduct eggs on 6th September. A clutch taken at Kafue Hook hatched on 8-17th December (Taylor, 1957). The late P. I. R. Maclaren (30.1.56) again confirmed that hatching takes place during the early rains in Northern Rhodesia.

TABLE 18

Breeding dates : Northern Rhodesia

<i>Locality</i>	<i>Clutch Ser. No.</i>	<i>Date found</i>	<i>Condition</i>	<i>Estimated laying date</i>
Bangweulu : L. Chali ..	NR. 1	21. 8.56	shelled oviduct eggs	24. 8.56
" L. Bumba ..	NR. 2	30. 8.56	unshelled oviduct eggs	15. 9.56
" L. Bumba ..	NR. 3	30. 8.56	shelled oviduct eggs	2. 9.56
" Chambesi R. ..	NR. 4	1. 9.56	shelled oviduct eggs	4. 9.56
" L. Bumba ..	NR. 5	2. 9.56	shelled oviduct eggs	5. 9.56
" L. Bumba ..	NR. 6	2. 9.45	shelled oviduct eggs	5. 9.56
Mweru Wa Ntipa : Katema ..	NR. 7	13. 9.56	c. one week	6. 9.56
" " Katema ..	NR. 8	13. 9.56	new laid	12. 9.56
" " Kampinda	NR. 9	14. 9.56	unshelled and shelled oviduct eggs	22. 9.56
" " Kampinda	NR. 10	15. 9.56	shelled oviduct eggs	18. 9.56
" " Kampinda	NR. 11	15. 9.56	shelled oviduct eggs	18. 9.56
Kalungwishi R. : Olandi ..	NR. 12	18. 9.56	shelled oviduct eggs	21. 9.56
" Olandi ..	NR. 13	18. 9.56	shelled oviduct eggs	21. 9.56
" Olandi ..	NR. 14	18. 9.56	shelled oviduct eggs	21. 9.56
Kafue Flats : Chimwajila ..	NR. 15	22. 8.57	unshelled and shelled oviduct eggs	28. 8.57
" " Iyeshya ..	NR. 16	30. 8.57	shelled oviduct eggs	1. 9.57
Kafue R. : Kafue Hook ..	NR. 17	7. 9.57	new laid	7. 9.57
Luangwa R. : ..	NR. 18	25. 9.57	new laid	24. 9.57
Upper Zambesi : Mongu ..	NR. 19	10. 9.57	shelled oviduct eggs	13. 9.57
" " Mongu ..	NR. 20	12. 9.57	shelled oviduct eggs	15. 9.57
" " Mongu ..	NR. 21	13. 9.57	shelled oviduct eggs	16. 9.57
" " Mongu ..	NR. 22	16. 9.57	shelled oviduct eggs	19. 9.57
" " Mongu ..	NR. 23	16. 9.57	shelled oviduct eggs	19. 9.57
" " Mongu ..	NR. 24	18. 9.57	shelled oviduct eggs	21. 9.57
" " Mongu ..	NR. 25	18. 9.57	shelled oviduct eggs	21. 9.57

Environmental factors

In all localities the breeding season is found to coincide with changes in one environmental factor, namely, the water level. Figs. 21-25 and 27 show (a) the breeding season ; and (b) the annual fluctuations in water levels—for six localities and over a period of several years—plotted from data supplied by the Water Development Department, Entebbe (Stations at Jinja and Fajao), and by the Water Development and Irrigation Department, Hydrological Section, Northern Rhodesia (Stations at Samfya, Mofwe, Namwala and Lukulu).

It will be seen that in all localities (other than northern Lake Victoria) the eggs are laid during the dry season at a time when the water level has already been falling for several weeks ; that some part of the incubation period coincides with the phase of lowest water ; and that hatching occurs after the onset of rains when the lakes and rivers are again rising into flood.

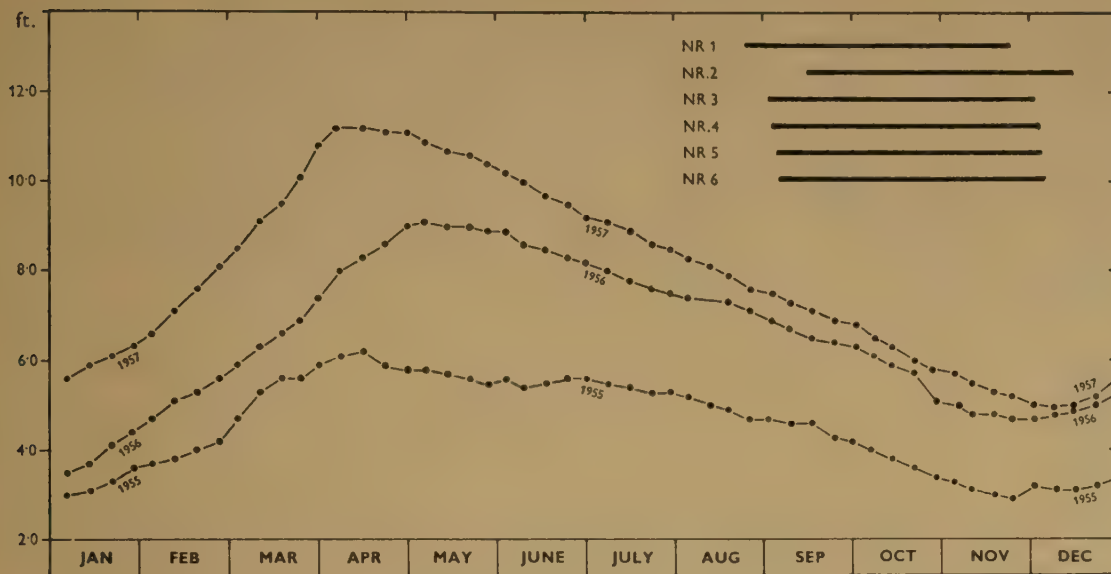


Fig. 21. Breeding records for *C. niloticus* from Bangweulu Swamp. Water levels are those recorded at Samfya for the years 1955-57.

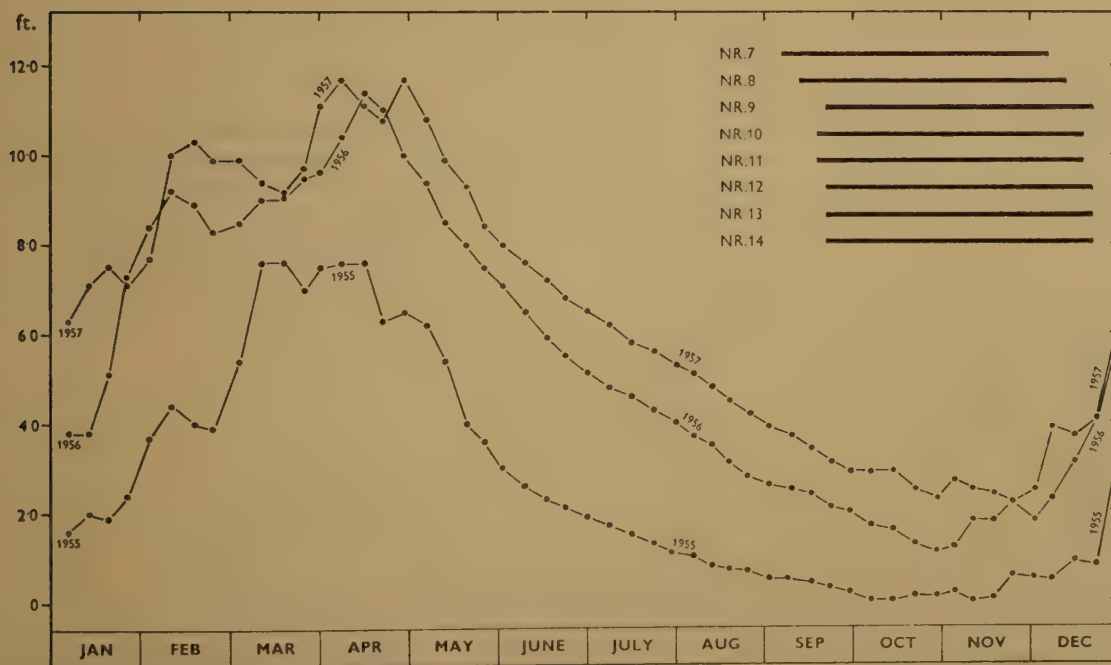


Fig. 22. Breeding records for *C. niloticus* from Mweru Wa Ntipa and Kalungwishi River. Water levels are those recorded at Mofwe for the years 1955-57.

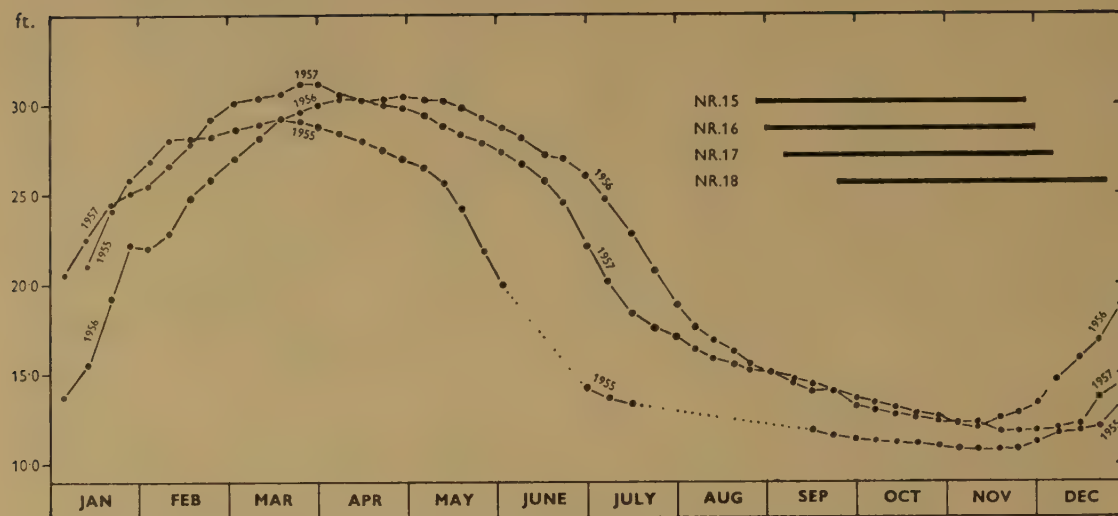


Fig. 23. Breeding records for *C. niloticus* from Kafue Flats and Luangwa River. Water levels are those recorded at Namwala for the years 1955-57.

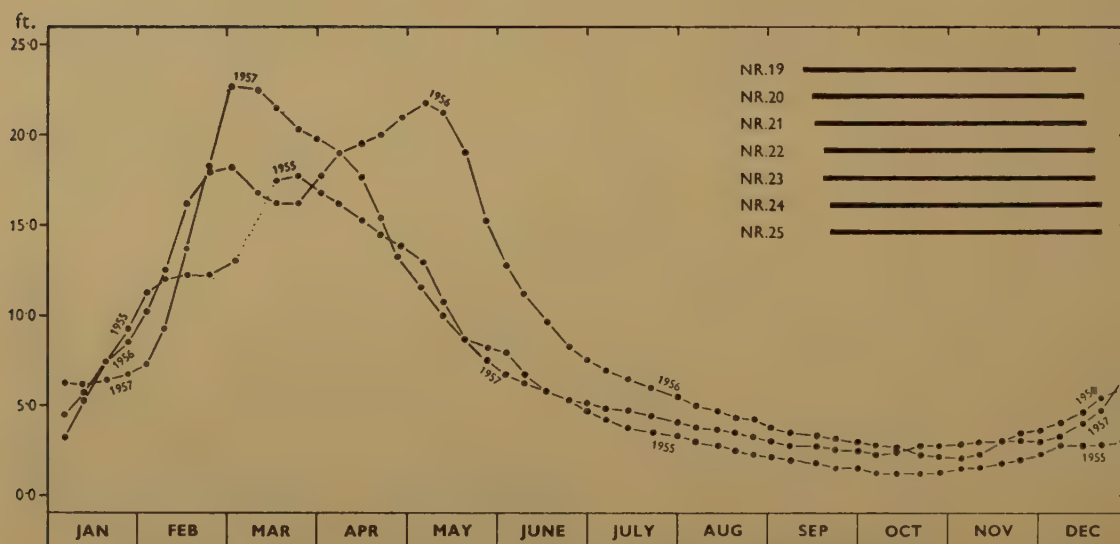


Fig. 24. Breeding records for *C. niloticus* from Upper Zambesi, Barotseland. Water levels are those recorded at Lukulu for the years 1955-57.

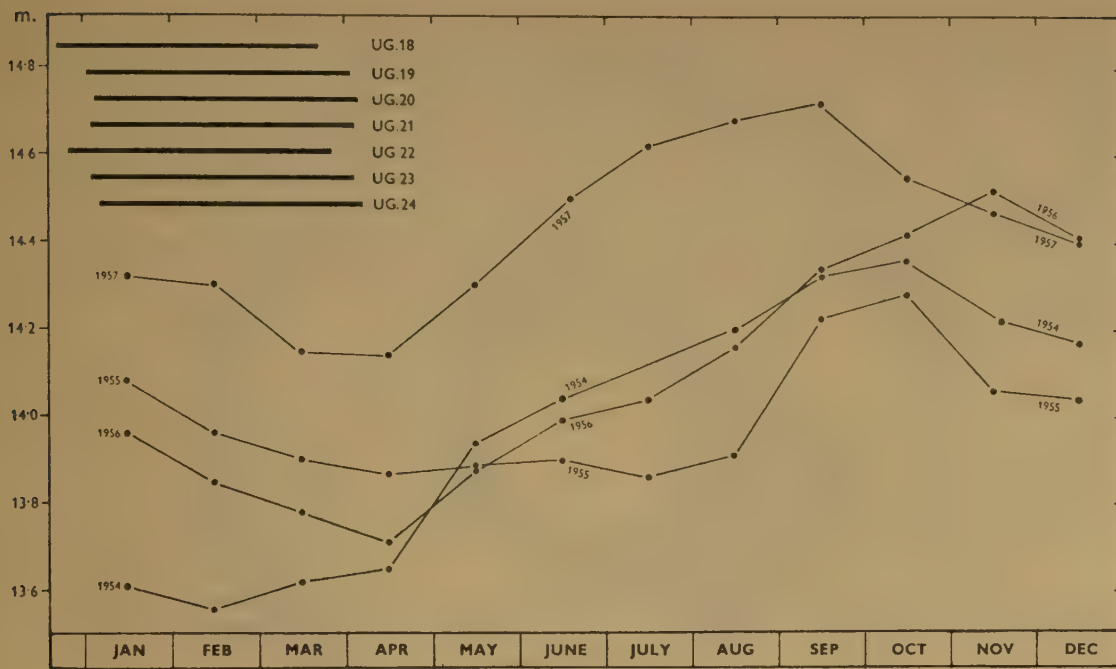


Fig. 25. Breeding records for *C. niloticus* from Victoria Nile below Murchison Falls. Water levels are those recorded at Fajao for the years 1954-57.

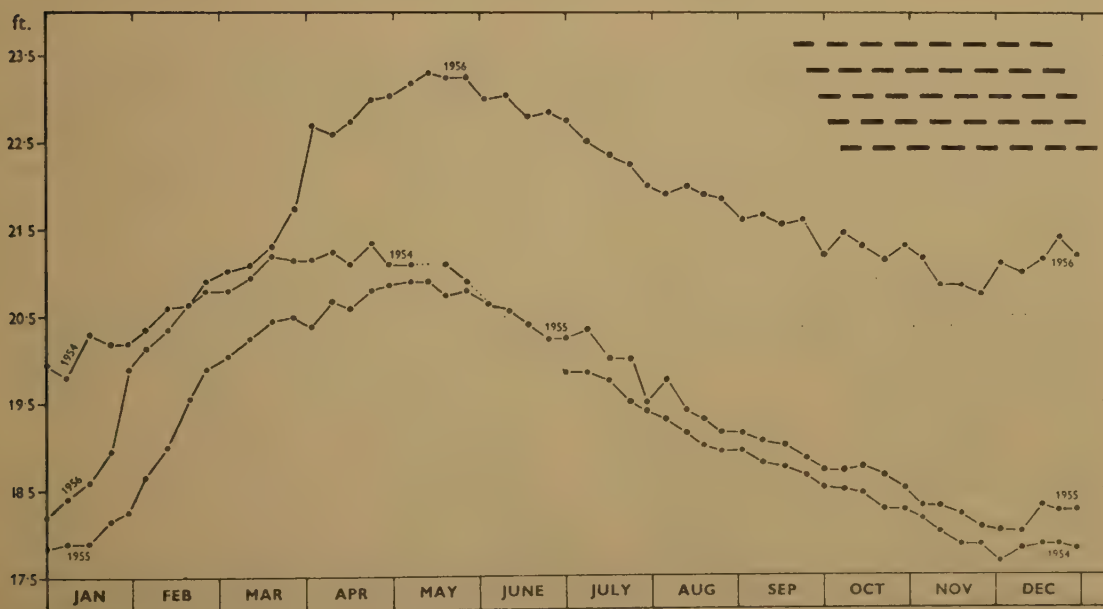


Fig. 26. Breeding season of *C. niloticus* in Lake Nyasa. Water levels are those recorded at Fort Johnston for the years 1954-56.

The correlation between breeding and climatic cycles also obtains in certain localities which lie outside the scope of the present survey. Thus Mitchell (5.6.57) reports from Lake Nyasa : " Nests containing new laid eggs can be found from about the 20th September into the first week of October. I have examined many nests near Karonga in the Northern Province, Domira Bay in the Central Province, and Fort Johnson in the Southern Province, and the breeding season holds over the whole lake." Mitchell has supplied me with data for water levels in Lake Nyasa (Station, Fort Johnson). The cycles in this lake are shown graphically in Fig. 26.

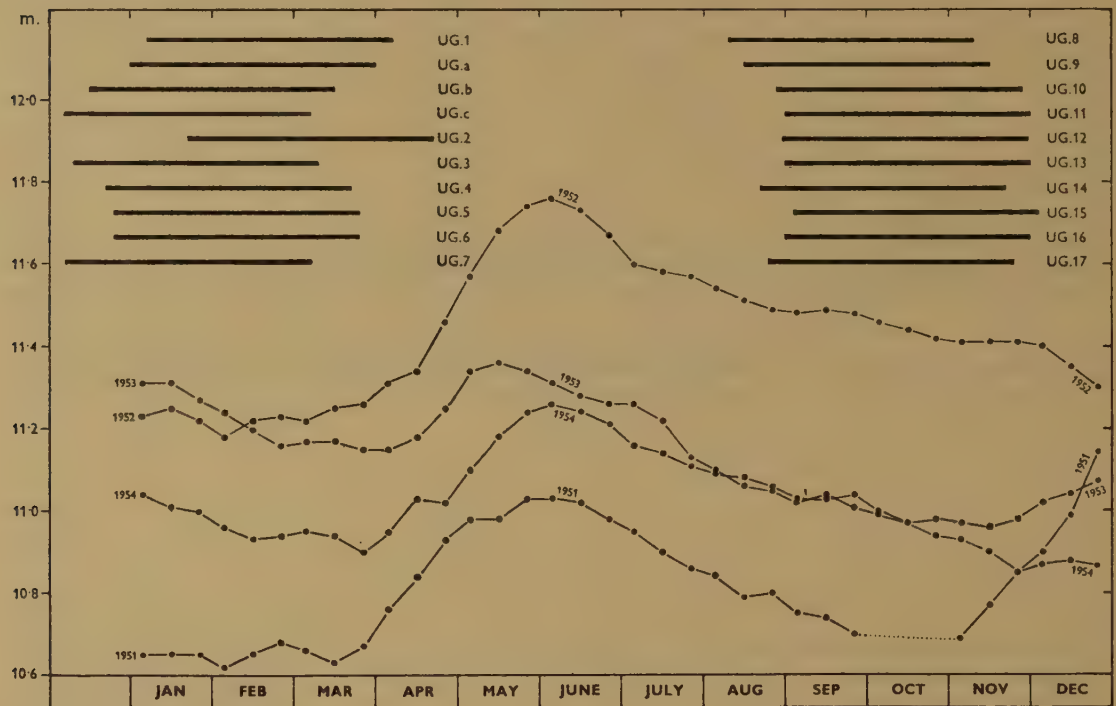


Fig. 27. Breeding records for *C. niloticus* from Lakes Victoria and Kioga. Water levels are those recorded at Jinja for the years 1951-54.

The situation in northern Lake Victoria is complicated by the ill-defined wet and dry seasons—which occur twice annually. Mean monthly rainfall data for Entebbe, over a period of 55 years, are as follows (Annual Report, 1951, East Africa Met. Dept.) :

Jan. 2.69 ins.	Apr. 10.26 ins.	July 2.98 ins.	Oct. 2.76 ins.
Feb. 3.46 „	May 9.38 „	Aug. 3.02 „	Nov. 5.08 „
Mar. 6.31 „	June 4.71 „	Sept. 2.93 „	Dec. 4.53 „

The relation of the breeding season in northern Lake Victoria to monthly rainfall is shown diagrammatically in Fig. 28. The lake water reaches its lowest level in February-March, but there is a second low water period in October-November. The two incubation periods are here again synchronised with the time of low water, and the laying periods with falling, and the hatching time with rising levels (see Fig. 27).



Fig. 28. Diagram showing the relation of breeding seasons of *C. niloticus* in northern Lake Victoria to seasonal changes in rainfall. Rainfall data are taken from East Africa Met. Dept. Annual Report 1951 and show monthly average for 55 years.

As is well known, in many other animals the reproductive cycle is in some way correlated with the seasonal rhythm of rainfall. In tropical regions especially, where dry and rainy seasons alternate, the breeding of birds and other animals is adapted to this environmental variant. In such cases, nesting normally occurs after the first heavy rains. For example, in Australian birds of many orders, reproduction is influenced or controlled by the breaking of the monsoon (Matthews, 1910-27; Marshall, 1954; Keast & Marshall, 1954). This connexion between precipitation and breeding is strikingly illustrated in Ceylon, where the north-east and south-west monsoons affect the island, and so affect the breeding season, at different times of the year (Baker, 1938).

In other species, rainfall affects the breeding season in an opposite, and indirect way. Such birds breed in the dry season and appear to respond to falling water levels and the consequent emergence of suitable nesting sites. For example, in Bear Island, Lack (1933) found that the breeding time of the Arctic Tern (*Sterna macrura*) was influenced by the condition of the nesting place, and that where low-lying grounds were flooded by late melting snow ovulation might be deferred for over three weeks. Similarly, the Australian Pelican (*Pelecanus conspicillatus*) is reported by MacGillivray (1923) to breed on islands that form as the floods subside—the laying dates coinciding with the progressive exposure of nest sites.

The Southern Carmine Bee-eater (*Merops nubicoides*) which nests in steep river banks left exposed in the dry season, is found breeding in late September in Nyasaland, in the first half of October in Portuguese East Africa, and in early November on the Zambesi (Chapin, 1939): in the Luangwa Game Reserve, Northern Rhodesia, we found these birds nesting in late September. These dates roughly coincide with the time of low water.

The Pied Kingfisher (*Ceryle rudis*) is another river-bank nester which makes its burrows as soon as the water level has fallen far enough for it to do so. It breeds in early May in Egypt (Meinertzhagen, 1930) and in August onwards in South Africa (Macworth-Praed & Grant, 1952-55). In India this kingfisher nests from November to March "after the rains have ceased sufficiently long for the rivers to fall and expose their banks and before they rise enough to flood the nest-holes" (Baker, 1932-35). The Indian Sand Martin (*Riparia riparia*) nests similarly and during the same months.

Another Indian kingfisher, *Halcyon smyrnensis*, breeds in February and March in rivers subject to spring floods, the young being fledged before the melting snows cause the first rush of water; but in the banks of canals, which are not subject to flooding, the laying season is two months later (Baker, *ibid.*).

In all these cases reproduction is in some way related to falling levels and to the emergence of suitable nesting places, as also in the case of the Nile Crocodile. Indeed, in *M. nubicoides* the parallel is close, both bird and reptile nesting at approximately the same time of year in the same river beds. Again, an alternative breeding season, such as obtains among crocodiles in Lake Victoria, has also been recorded among birds. An example is the Wood-swallow (*Artamus melanops*) of Western Australia, which nests in February and March, or in June and July, or at both times, according to the rainfall (Robinson, 1933)—though in this case nesting is related to precipitation, rather than drought.

It is not known how the seasonal variants achieve their effect in the crocodile, and no experimental work has been done on this problem. Nor is it possible to say what is the extrinsic regulating factor—whether drought, temperature, insolation, water level or the psychological effect of available breeding grounds. An environmental factor which may be considered of importance is falling water, but there is no proof that this variant *per se* stimulates ovulation.

On the other hand, the biological advantages resulting from the habit are evident. (1) Crocodile eggs are known to be sensitive to moisture (Voeltzkow, 1893); and they would in any case be destroyed if the nest was flooded. Yet they must be located near enough to permanent water to allow easy access to the young on hatching. The siting of the nest and the timing of the incubation period are both nicely adjusted to meet these requirements. (2) We have seen that the hatching time normally coincides with the breaking of the rains, and thus with rising floods. This timing affords optimum conditions for the newly-hatched young, because the inundation of the plains facilitates their dispersal and opens up new retreats and feeding grounds in the wide-spreading shallows; while the rains are followed by a rich harvest of insect food on which the early young subsist.

BREEDING BEHAVIOUR

Territory and combat

Little is precisely known regarding territorial behaviour in the breeding season. However the fact is well established that inter-male rivalry frequently finds expression in combat (see p. 307). Pitman (1931, 1941, 1942) states that crocodiles are notorious for fighting among themselves, and that where they are abundant they indulge in terrific contests, which often terminate fatally. Mr F. Wilson tells me that he has himself seen two large crocodiles, which he believed to be males, fighting in the water, in Kadam Bay.

What is not clear, however, are the circumstances under which these contests take place. Some of the inter-male fighting at breeding time may be for the possession of mates. According to Deraniyagala (1939) males of *C. porosus* are said to fight each other for the females; Clarke (1891) refers to fierce battles among males of *A. mississippiensis* in the breeding season; and Bartram (1791) gives a graphic description of a fight he witnessed.

On the other hand, fighting in defence of territory does occur, at any time of the year, the area so defended being a basking-ground or feeding-place. Below Murchison Falls, particular individuals were seen in possession of the same basking site on different occasions. And several instances are known of a large male taking possession of a favourite watering place, from which it will drive away all rivals (Stevenson-Hamilton, 1954; Pitman, 1931). For example, the famous "Lutembe" of Entebbe, which would come for food when called and always occupied a particular part of the water-front, for years drove away rivals and thus ensured the safety of his domain, until, in old age, he was no longer able to do so.

Vocalization

Crocodiles utter a variety of sounds, at different periods of the life-history and under different circumstances.

(1) There is the yapping or croaking call—"umph" or "aõ" of the unhatched, or newly-hatched young, which is the signal for maternal help, or, after birth, a distress signal.

(2) A sharp, coughing hiss is uttered as part of the threat display when a crocodile is cornered and unable to make its escape to the water. This was observed by me in the Luangwa Game Reserve, and similar behaviour has been reported by Player from Zululand.

(3) A low growl is sometimes heard when a female is surprised guarding her eggs (Charles Magala, pers. comm.). Hippel tells me that a crocodile caught in a trap will, when approached, growl like an angry bull.

(4) Wounded crocodiles sometimes utter a bellow of pain; and Pitman's report (unpub. notes) of an eleven-foot female which he shot at Lwera, and which "died bellowing in the swamp," proves that loud vocal effects are not confined to the male sex.

(5) During the breeding season, basking males often bark or cough, as I heard them do on many occasions at Magungu, the note being deep, loud, hollow and abrupt.

(6) The most powerful and remarkable demonstration of a crocodile's repertoire is the full roar. The animal, which has been lying on the mud with jaws agape, first elevates its head and opens its jaws yet wider in what appears to be a prodigious yawn (Plate 4, fig. 2). The roar is a growling rumble, very deep in pitch, rattling, vibrant and sonorous, like distant thunder or the roll of a big drum, which is protracted and may persist for six or seven seconds. Jobson (in Cuvier, 1831) gives an apt comment when he speaks of the sound as if coming from the bottom of a well.

In my experience, roaring is only heard in the breeding season. It is generally believed that the roar is an attribute of the male, but it is not certainly known whether the female responds vocally. Judging by the large size of animals seen roaring on the grounds at Magungu and Fajao, these were undoubtedly males. In this connexion, Schmidt (1919) states: "Though I have never had conclusive proof that females were not endowed with so strong a vocal organ, in several instances bullets snuffed out the lives of actual performers and they proved to be males."

While the biological function of the roar is not clearly understood, from the available evidence it appears to be a mating call directed towards members of the opposite sex, rather than a threat directed against rivals. In the first place, it is known that the call does attract crocodiles to the caller: indeed, in 1952 there was a native at Butiaba who collected crocodiles for sale by imitating the roar with vocal and drumming effects. Again, in reference to the reduction of crocodiles resulting from his campaign against females on the breeding grounds in Lake Victoria, Pitman (1948) has pointed out that unless the males attract the females, it is difficult to account for the continued replacements of casualties to the adult female stock. A case is also reported from the Belgian Congo by Schmidt (1919) of a large solitary male which announced its presence by bellowing, and was later joined by two other crocodiles. Hippel told me he believes the female also calls the male—the sound being a growling roar rising to a crescendo and quite distinct from the male's roar.

Copulation

Copulation of the Nile Crocodile has very rarely been witnessed in the field; and nothing useful has been published on the subject. Sonnini (1800) was certainly mistaken in believing that during congress the female is turned upon her back ashore. Equally improbable is the report of Sinhalese crocodile hunters that, in *C. porosus*, "copulation is effected by both animals raising themselves in an embrace in shallow water, the forequarters in the air, the jaws usually interlocked" (Deraniyagala, 1939).

On January 1st, 1956, from the Magungu hide, I witnessed the preliminaries to pairing. At 2.54 p.m., while attending to one of the cameras, I heard splashing

and commotion in the water but a few yards away, where two crocodiles were lying in the shallows. The smaller of the pair then thrust her head and fore-quarters high out of the water, the mouth widely agape and pointing heavenwards, and uttered a creaking or groaning sound. Immediately afterwards the male, who had been lying awash, reappeared at the surface, approached his mate from behind, and mounted her. Then both crocodiles moved off into deeper water and submerged together.

On several previous occasions at Fajao crocodiles near the opposite shore had been seen to rear high out of the water, and with the head pointed towards the sky, indulge in a prolonged yawning display, but at the time I had not appreciated the possible significance of this demonstration—as a pre-nuptial display by a breeding female. This interpretation is supported by observations (then unknown to me) of Dharmakumarsinji (1947), who witnessed a somewhat similar display in *C. palustris* on the Shetrunji River. As one crocodile (sex not noted) came close to its partner, he says : “ I distinctly saw it with closed mouth raise its head and neck high out of the water, pointing its snout at an angle of about 70 degrees for a few seconds.” Copulation followed the display, near the surface in deep water.

In Northern Rhodesia a member of the Game Department witnessed copulation in *C. niloticus*; and in response to enquiries Major W. E. Poles (5.2.57) has been kind enough to send the following particulars which, on account of the rarity of such observations, I quote in full. “ A young ranger named Hough, who was drowned by a crocodile shortly afterwards, accompanied me on a long tour down the Luangwa in July and August, 1951. On the 2nd August he was watching crocodiles where the reptiles are very plentiful and witnessed the mating of two large ones. He described how one was basking in the shallows, with its head and shoulders out of the water, resting on a sand bank. Another crocodile appeared from deep water and swam alongside. The basking crocodile, which seemed to be the female, rolled over, exposing her belly and the male covered her with his shoulders. The female rolled over again and the male mounted her and copulation took place. . . . The mating took place in shallow water and lasted only a short time, after which both crocodiles returned to deep water and submerged. They made no vocal sound. At the time I was unaware of the importance of Hough’s observation or I would have questioned him more closely and made detailed field notes”.

Apart from the above observations, little is known. When questioned, Wajalubi assured me that in his experience copulation takes place in the water ; and he also stated that a female on land which is ready to mate, raises up the tail as she goes into the water. Wosseler (1915), who observed courtship of *C. niloticus* in Hamburg Zoological Gardens, reports a “ gasping roar ” during copulation. And Descourtilz (1809) also states that *C. americanus* roars during copulation.

NESTING ACTIVITY

The nest site

Choice of a nesting site is governed by three factors : (1) a sufficient depth of soil to provide a pit where the eggs can be deposited ; (2) nearby shade into which

the guardian mother can retire during the heat of the day ; and (3) access to permanent water.

Soil

The eggs are usually found in the coarse sand of spits, riverside mud-flats, low-lying islets, lake-side beaches, or in the bed of a dried watercourse. But in rocky habitats, where deep earth is not available, crocodiles will lay in shallow gravel beds : this was the case both on Katema Island in Mweru Wa Ntipa, and on precipitous rocky islands near Bugondo, Lake Kioga. At Kigi Island in this lake the reptiles had to climb steep stone screes to reach the nesting ground at the summit, some fifty feet above the water. In 1956-7, along the Murchison reach of the Nile, several females were found nesting in isolation away from the main grounds, high up on precipitous, eroded banks (Plate 7, fig. 1).

Shade

A crocodile cannot lie exposed to the full glare of the sun for protracted periods : hence nearby shade or cover, from which the female can continue to watch over the eggs, is essential. In Uganda the sites—while differing greatly in other respects—were almost invariably on dunes overgrown with scrub, in lake-side thickets or near the fringing forest, beside isolated forest trees, or beneath an overhanging cliff. This need for shade is confirmed by the experience of Hippel (pers. comm.) and Pitman (unpub. notes). In Northern Rhodesia, however, Attwell told me that nests were sometimes dug in the open, and in September 1957 we found one nest far from any adequate cover, on top of an exposed sandhill of the Luangwa River.

Water

The nesting grounds are usually within easy reach of permanent water. But in dry water courses of the Murchison Nile some nests were found over a hundred yards from the main river. Savidge (27.4.57) also reports four nests from the Nansika tributary which were 200 yards from the river. A nest at Buvu Island was separated from the lake by a 200-yard belt of impenetrable fringing forest. And Charles Magala assured me he had known crocodiles to go about 400 yards from water to reach a suitable nesting place.

Colonial sites

Where crocodiles are entirely free from disturbance, and allowed to breed as they have doubtless done from time immemorial, they nest gregariously, the nests lying so close together that, after hatching time, the rims of the craters are almost contiguous. At Ntoroko peninsula (Fig. 29), between the Wasa and Muzezi Rivers, S. Lake Albert, two such communal sites still remained in 1952. Here

in April I found many craters—the young having hatched—spaced apart, somewhat like Sandwich Terns' nests in territories, in places only three to four yards from centre to centre. In one colony, near the sandspit at the north end of the peninsula (Fig. 30), seventeen craters were found in an area 25 x 22 yards; in the other (Fig. 31), in dunes a mile south, between the Muzezi and a lagoon, twenty-four craters were concentrated in an area 26 x 24 yards.



Fig. 29. Sketch map of peninsula between the Waza and Muzezi Rivers, at Ntoroko, Lake Albert. The arrows indicate the position of two colonial nesting grounds.

In the thirties, Pitman knew many such communal grounds in Lake Victoria. On the Buvu site (since deserted) he told me he had seen about thirty nests. Colonial nesting has also been reported from other parts of Africa. Thus Grabham (1909) found three nests, about a yard apart, in the bed of the Rahad River, a tributary of the Blue Nile; and Adamson (1955) has published a photograph of a communal site on the uninhabited island in Lake Rudolf, which shows nine or ten craters dispersed at intervals of about two yards. In Nyasaland, Mitchell (1946) reports finding six nests in an area ten yards square, and nearby the crowded nests could not be counted as they were overlying each other.

This aspect of the nesting behaviour is of special interest, since the colonial habit is probably normal for the species. But it is incompatible with present-day disturbance. In most areas the breeding population has been depleted, the ancestral nurseries are deserted, and the crocodiles that survive are dispersed. Meanwhile, we remain almost ignorant of the ecology of breeding crocodiles in their former state of abundance. For example, it is not known whether, on the communal

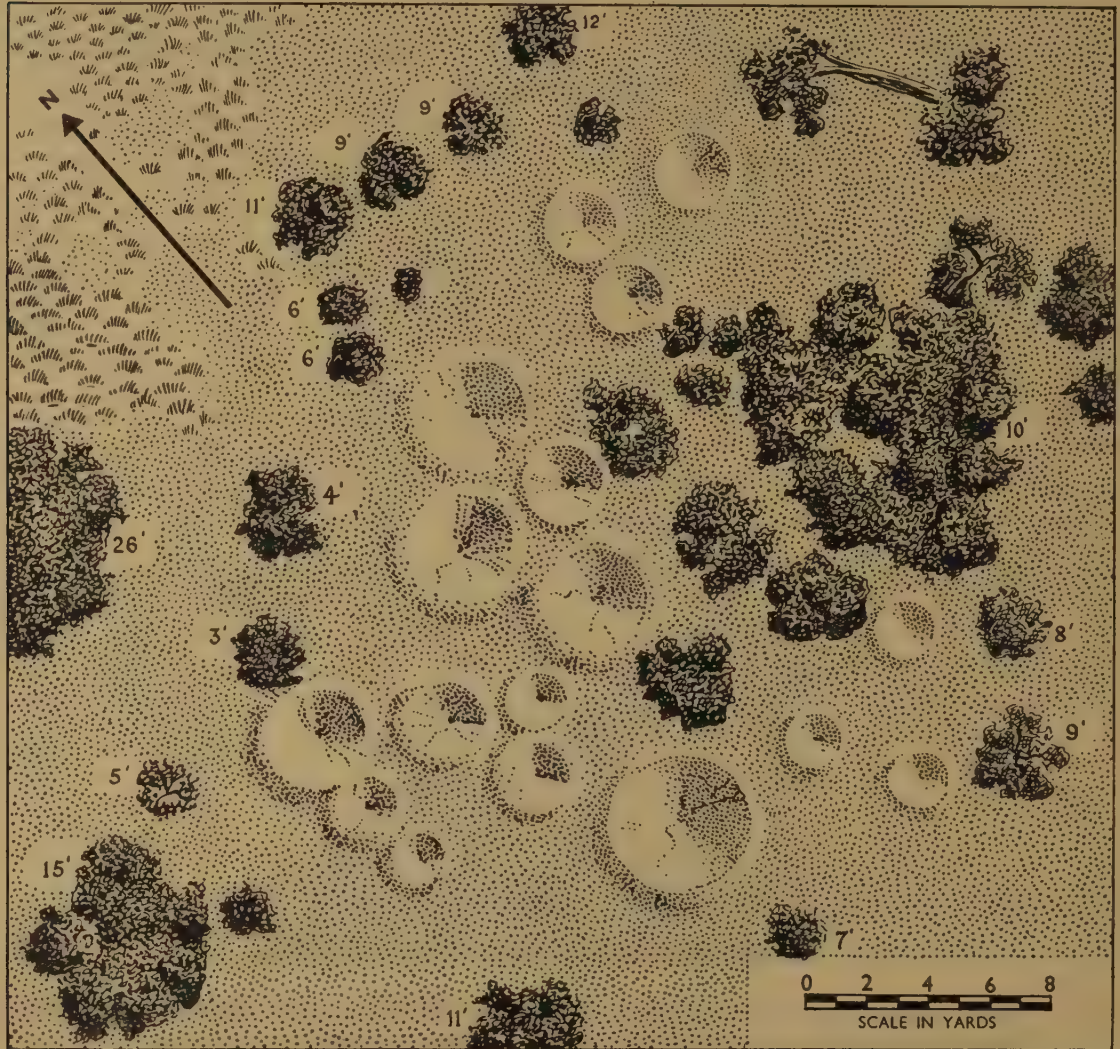


Fig. 30. Colonial nesting ground at A (See Fig. 29) : showing diameter and proximity of excavated nests and position and approximate height of shade trees and bushes.

grounds, a female occupied and defended the territory round her nest ; whether she covered her own clutch or lay on the grounds indiscriminately ; whether the site was guarded by all the females that had nests there, or by a few members of the group. Nor is anything certainly known of conditions at night—whether the grounds were occupied or deserted ; nor of the relations between breeding females to each other and to the young when the eggs were hatching. With the rapid changes now taking place all over Africa, such questions relating to the primeval breeding behaviour may well remain unanswered.

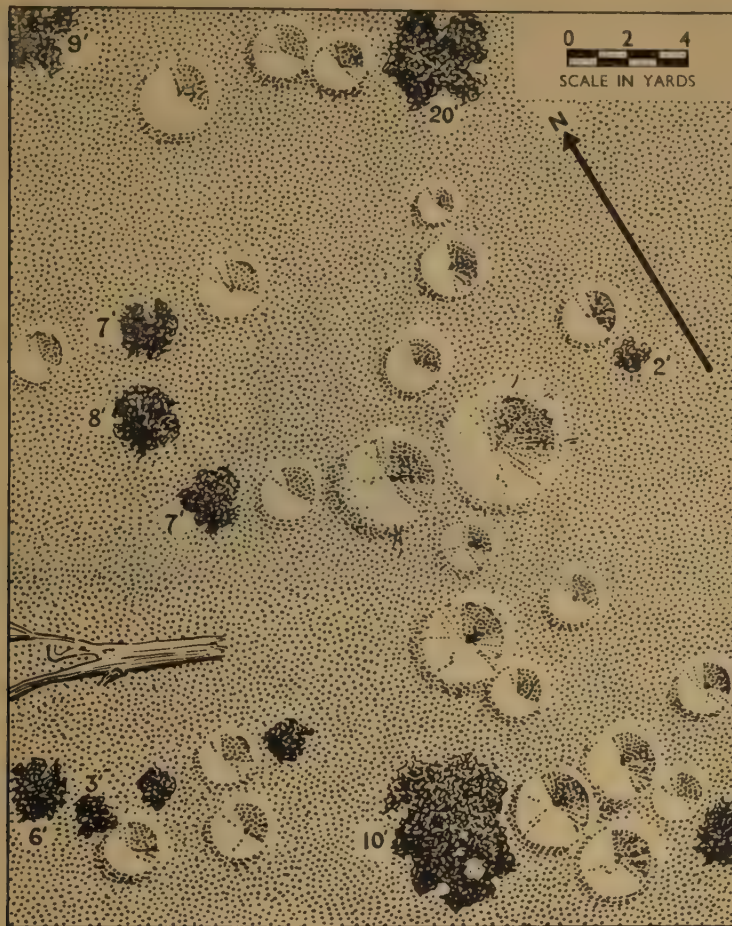


Fig. 31. Colonial nesting ground at B (See Fig. 29) ; other details as in Fig. 30.

Egg laying

Little is precisely known of the female's procedure at laying time. Observations of Voeltzkow (1899) suggest that the eggs are deposited at night, as are those of marine turtles, such as *Chelonia midas* (Hendrickson, 1958) and *Dermochelys coriacea* (Tweedie, 1953), or shortly before dawn. A game guard reported to Major G. E. Taylor that he had seen a crocodile digging its nest near the river at Kafue Hook "in the early morning," 5th September, 1957 : eggs were found in the nest two days later.

Where there is a sufficiency of sand, the female digs a hole about two feet deep, and lays the eggs in tiers. During the process sand falls, or is shovelled, among the eggs, so that though closely-packed they are yet separated, more or less, from one another, like the currants in a cake. The upper eggs are generally about one foot beneath the surface ; but in gravel they are sometimes scantily covered, and in such situations the eggs are tightly packed and the shells often dented.

After laying the female fills in the cavity with earth and leaves the surface flush, so that, save for tracks or the imprint of her belly shields, no sign of the nest remains visible.

Clutch size

Clutches over 80 are uncommon, and over 85 rare. Wilson & Felkin (1882) record a nest of 82 eggs from the Sudan ; L. E. Vaughan (29.3.56) reports 87 eggs from Northern Rhodesia ; and L. Trollope found a clutch of 92 eggs on the Chobe

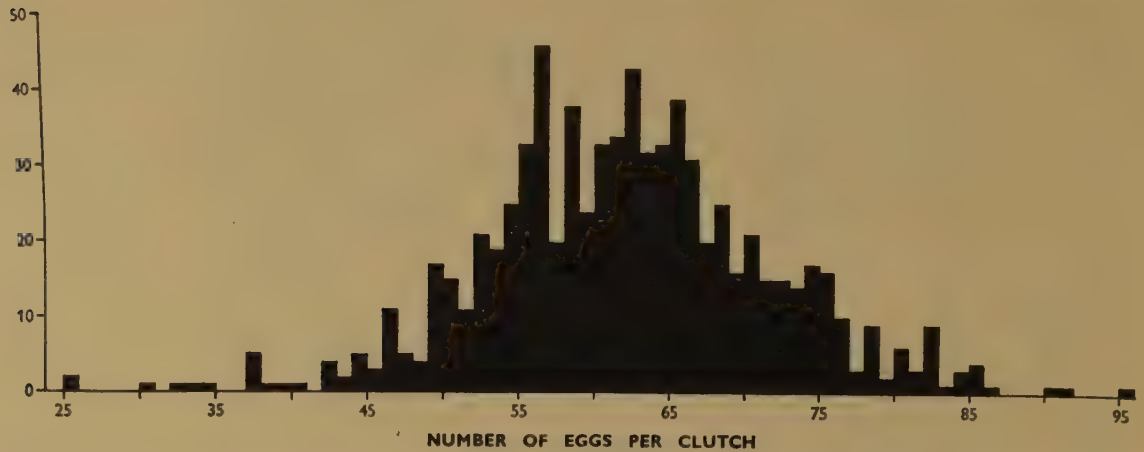


Fig. 32. Histogram showing clutch-size frequency distribution for 775 nests in northern Lake Victoria. (Pitman's unpublished notes.)

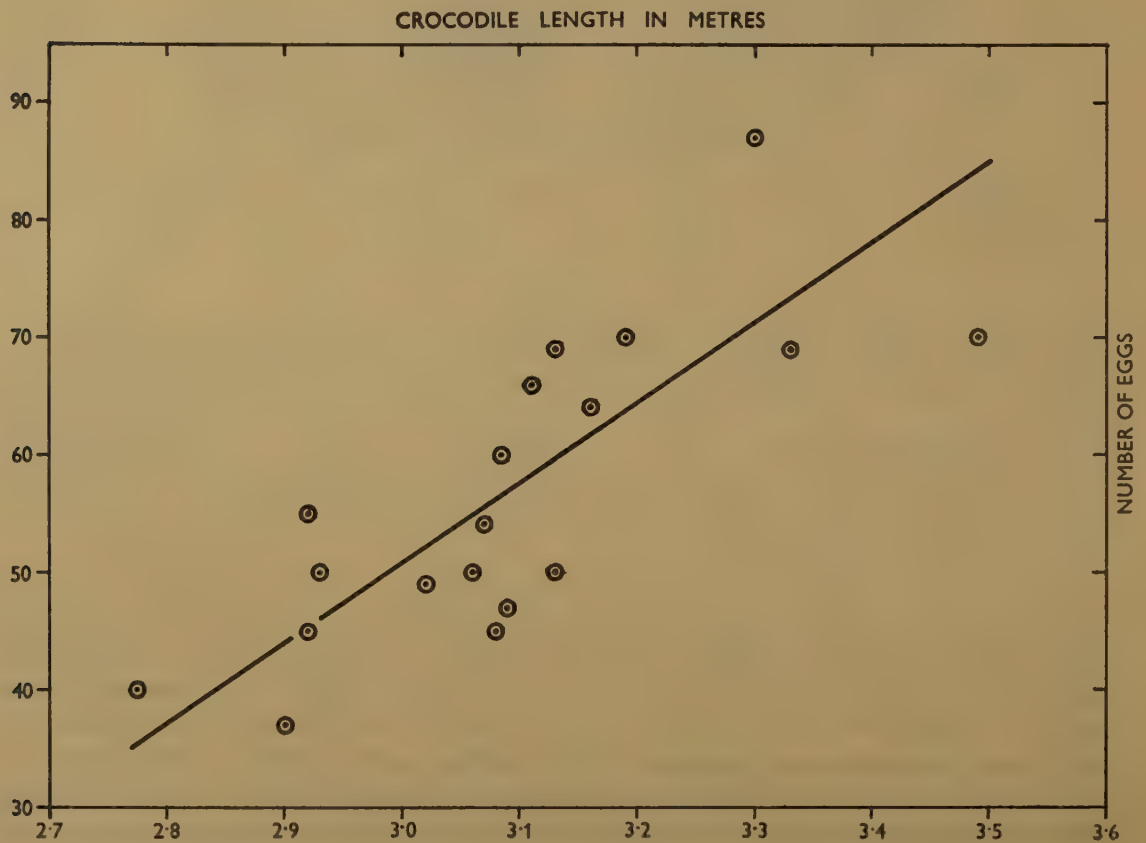


Fig. 33. Scatter diagram showing relation between clutch size and length of female.

River. Crocodile No. 321, shot on the Kafue, contained 87 shelled oviduct eggs. Yet larger clutches are recorded by Pitman, who found three nests in Lake Victoria containing 90, 91 and 95 eggs.

Pitman made a large series of observations on the size of clutches destroyed by him and he has most kindly allowed me to make use of the following data which I have taken from his unpublished annual records. Between the years 1940 and 1949 clutch counts for 775 nests show an extreme range from 25 to 95 eggs, with an average of 60.4 per nest (Fig. 32). My own records show an average of 54.9 eggs for seventeen clutches in Uganda, and of 56.2 for twenty-three clutches in Northern Rhodesia and Barotseland.

Though scanty, the present observations seem to show some correlation between the number of eggs laid (but not the size of the eggs) and the size of the parent—large crocodiles laying the larger clutches (Fig. 33).

Incubation period

The incubation period of *C. niloticus* is generally stated to be about ninety days (Pitman, 1936), as compared with seventeen or eighteen weeks for *C. palustris* (Schultze, 1914), and nine weeks for *A. mississippiensis* (McIlhenny, 1934).

In 1957, at several sites below Murchison Falls, laying commenced in the first week in January. At my suggestion, Mr John Savidge kindly continued observations when I had to leave. He reports (27.4.57) that by 31st March twelve nests on the Nansika tributary had been excavated by the parents, and four were still unhatched. On the same day at another nesting ground he found eleven excavated nest-craters and two females still "sitting". These observations fix the incubation period at between twelve and thirteen weeks.

PARENTAL CARE

Nest guarding

Crocodiles found covering the eggs are always females. During the whole incubation period the mother remains in attendance—either lying over the nest with the lower throat or thorax above the eggs (Plate 7, fig. 1), or in nearby cover. Wajalubi told me (1952) that the females remain on the grounds by night as well as by day. This may well be the case, for it appears almost certain that brooding females fast. Hippel informed me (1952) that he had never found food in the stomachs of females taken at the nests. Pitman's experience was similar (1930). Stomachs of nesting females examined by me were likewise empty.

During this period—and, in my experience especially when nesting at some distance from the water—the females become torpid and are most reluctant to leave the grounds even when approached. For example, I came upon one female in a ravine below Murchison which refused to stir even when large stones were thrown on her back, and when finally driven off, instead of making for the river, she merely crawled a few yards away into dense bush. Pitman (unpub. notes),

Hippel (pers. comm.) and Savidge (27.4.57) all refer to this strange "trance-like" condition of brooding crocodiles, which seems similar to the state of aestivation which has been recorded of crocodiles in other circumstances.

Release of the young

The young croak as hatching time approaches, and this is the signal for the mother to uncover and so liberate her offspring. As with many other aspects of the breeding biology, details of the process have rarely been observed. Mr L. J. Sim, a crocodile hunter in Tanganyika, informs me that on the 30th January, 1956, in Tanganyika, he saw a crocodile lying flat on its belly, wriggling and squirming. On reaching the spot he heard the young croaking from beneath a shallow depression that the female had made—the sand having been scooped out laterally. Next morning, broken shells were lying in the sand, and the young had gone. An African, named Stefan, told Sim that he had witnessed the same method of liberation, and he was most insistent that the feet were not used. This method is certainly consistent with the appearance of the broad and shallow nest craters that are found after the young have hatched: some of these basin-like excavations are over four yards in diameter.

Liberation by the female is necessary because, after three months' incubation and trampling, the earth above the eggs becomes compacted. At some nests opened by me the ground had to be chipped away with a knife and the eggs were set in a matrix as hard as mud-brick. Emergence through a foot or more of sun-baked and hard-packed soil would be impossible for the unaided young.

Care of the young

At hatching time, the female becomes bolder than usual, in defence of her offspring, and will even attack a man on land. Sonnini (1800) was told by an Egyptian who brought him some newly-hatched crocodiles that he had been attacked while collecting them. This observation may well be reliable, for similar instances have been reported of other species—*C. porosus* (Boake, 1870; Shelford, 1916); and *A. mississippiensis* (McIlhenny, 1934).

An interesting case of a crocodile (*C. palustris*) attacking enemies other than man is given by Dharmakumarsinji (1947), who watched a female for a whole day maintaining guard over its brood. "I saw this crocodile rush out of the water," he writes, "at least a dozen times, to drive away Black-necked Storks (*Xenorhynchus*), Herons (*Ardea*) and large Egrets (*Egretta*) when they ventured to alight near the young which were lying helpless at the water's edge."

There is also some evidence that the parental instinct lasts at least until the young crocodiles reach the safety of the water. In Nigeria, Lambron (1913) was told by natives that young crocodiles attach themselves to the dorsal fringe of the mother's tail and thus are conveyed to the water. Early authorities have also referred to maternal transport of the brood. According to Goldsmith (1805), when the young have been freed from the nest—"a part run unguided to the

water ; another part ascend the back of the female, and are carried thither in greater safety." Stefan also told Sim (personal communication) that "when the young emerge, they mount the back of the mother, and as soon as it is dark, she transports them through shallow water to a patch of reeds. Here the young instinctively cling to the reeds."

While these stories may not be entirely reliable, there is good modern evidence of some after-care. In Lake Victoria, F. Wilson once saw a female crocodile with seventeen or eighteen recently-hatched young sunning on a bank. As he approached the parent went into the water, followed by her offspring. H. Holloway assured me that on several occasions he has seen crocodiles in the Kabompo River near Ndola accompanying new-hatched young in the water—like a duck with her brood. Several of these escorting crocodiles were shot, and as the stomachs never contained young crocodiles, they were certainly not cannibals caught in the act. More recently I am informed by J. Savidge (27.4.57) that on the Nansika grounds below Murchison he saw young crocodiles all around an adult in the water ; and visitors to the same place later recorded babies resting on a crocodile's back.

EARLY LIFE

At birth the Nile Crocodile measures about 28 cms. The young have no immediate need of food, for a large quantity of yolk—about equal to that of a hen's egg—remains enclosed in the body, and provides a store of nutriment for several months. When eight weeks old, this yolk mass is still as large as a walnut ; and according to Pitman (1929) traces of it have been found after the age of six months.

The feeding habits of the young have been described elsewhere (see p. 293). The young are very agile from birth ; and, like their elders, when surprised ashore they make for the water and readily dive to avoid capture. At first they are strongly gregarious, each pack probably representing a family group : and as Pitman (1936) has pointed out : "They quickly disperse when frightened, but soon pack again, calling to each other loudly with a chirruping cry."

At this early period of life crocodiles are active climbers. Dr Hoare (in Pitman, 1929) saw them lying along overhanging branches of trees onto which they climb direct from the water. In Northern Rhodesia, L. E. Vaughan found them climbing up grasses and "hanging on like chameleons." N. H. Searle tells me that on the Lower Semliki he has seen them climbing in *Phragmites* to a height of six or eight feet, whence they drop off into the water at the approach of a canoe.

A few days after hatching the young lead a life of seclusion, shunning both the basking grounds and the open water, and seeking sanctuary from numerous enemies, including members of their own species, among the papyrus, in sudd, weedy shallows, backwaters, or in isolated pools—occasionally at some distance inland. A striking instance of this segregation of the young from their elders was seen at Magungu, where yearlings occupied a chain of shallow, weed-choked meres a mile back from the river. All those which I saw in the meres in 1956 were first-year juveniles (see p. 247) ; and J. R. F. Mills (1954) reported seeing small crocodiles "a foot or so in length" at the same place in 1953. By their

second year they have vanished, and their disappearance illustrates a curious and little understood phenomenon. For with growth, there follows a period when juveniles mysteriously disappear from the scene in all habitats. One sees those that have recently hatched, and again crocodiles of five feet and upwards. But although the intervening sizes can be shot in the shallows at night, their diurnal whereabouts remains an enigma. Many experienced hunters and naturalists have commented upon the absence of individuals measuring from about two to four feet in length. Pitman (1935) refers to this anomaly as "a conspicuous feature of African inland waters;" and elsewhere (1931) he writes: "One could almost believe that crocodiles of smaller size were non-existent and there was no intermediate stage." Hippel, with years of field experience as a professional hunter, told me he had never seen or taken young crocodiles between one-and-a-half and three-and-a-half feet. Magala's experience was similar. In areas, where under protection, crocodiles are still abundant, as below Murchison, in the Kafue and Luangwa Reserves, at Mweru Wa Ntipa, and Ndumu Reserve in Zululand, the apparent absence of small crocodiles seems the more remarkable. All that one can certainly say is that between the ages of about two and five years crocodiles go into retreat; and since they can have few enemies other than larger individuals of their own kind, it is probable that this cryptic behaviour has been forced upon them by the habit of cannibalism.

PART III. ECOLOGICAL AND ECONOMIC STATUS

FOOD AND FEEDING HABITS

A study of the food and feeding habits is a first essential in any attempt to assess the status of the crocodile in the ecology of inland waters. Such a study calls for the examination of stomach contents, which will provide not only a general picture of predator-prey relations, but will also afford a comparison between the habits of crocodiles of different sizes, and between those from different localities.

The present observations are based upon an analysis of stomach contents of 851 crocodiles from the following localities—the numbers here given refer to stomachs examined and (in brackets) those containing food: Uganda above Murchison Falls, 106 (95); Uganda below Murchison Falls, 34 (29); Bangweulu Swamp, 145 (110); Mweru Wa Ntipa and Kalungwishi River, 63 (49); Luangwa Valley, 98 (87); Kafue Flats, 101 (91); Upper Zambesi, 272 (212); Zululand, 32 (28). Most of this material was examined by me in 1952, 1956 and 1957. Also included are various records received from Mr F. Wilson and Mr P. H. Greenwood (L. Victoria), Mr H. Holloway (Bangweulu and Upper Zambesi), Mr Grobler (Bangweulu), and Mr H. H. Voigt (Zambesi). The records from Zululand were supplied by Mr I. H. Player.

Food in relation to growth

In a preliminary report on work done in Uganda in 1952 (Cott, 1954, a) attention was drawn to the fact that feeding behaviour and diet of the Nile Crocodile change markedly and progressively throughout life. From the present survey it is now

clear that these changes are of such magnitude—and this in every locality for which we have adequate information—as to make body-length a key factor in the crocodile's feeding ecology.

The proportional occurrence of different categories of food taken by crocodiles, in relation to length, is given in Table 19 ; and Fig. 34 presents these data, serially, for each prey category. A glance at the histograms will show that for almost

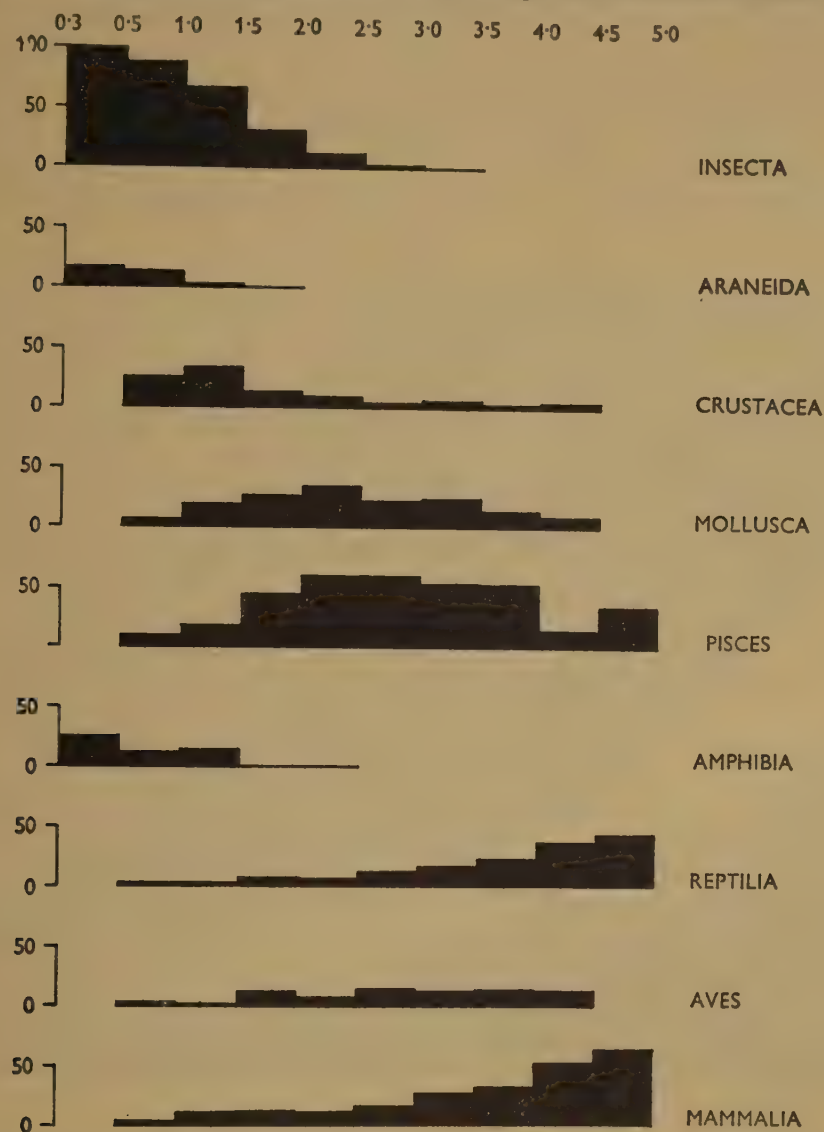


Fig. 34. Frequency of occurrence of different kinds of food, in relation to crocodile length. For each length group, occurrences are expressed as a percentage of stomachs containing food of any kind.

any type of prey (birds are an exception) the feeding pattern tends to change, often in a regular manner, throughout life. Three main patterns can be recognised ; and these are in accordance with what is known of the crocodile's changing habitat requirements.

(i) In the first, are prey for which the curve begins at its maximum and falls away to zero : this is the general intake pattern for insects, spiders and anura.

Such prey are captured by day and night, both in and above the water, by young crocodiles during the period when they lead a secluded life among waterside vegetation, papyrus debris, and weed-choked shallows.

(ii) In the second, are those for which the curve rises towards middle-life period, and falls away in old age : such is the frequency distribution for crabs, molluscs and fish—under-water prey which are captured mainly at night and often well out from the shore.

(iii) In the third, are those for which the curve begins low and rises steeply in old age : such a pattern is shown for reptiles and mammals—prey which may be captured by stealth and surprise when crocodiles are lying inshore or ashore during the daytime.

These various progressive changes in diet are illustrated in generalized form in Fig. 35.

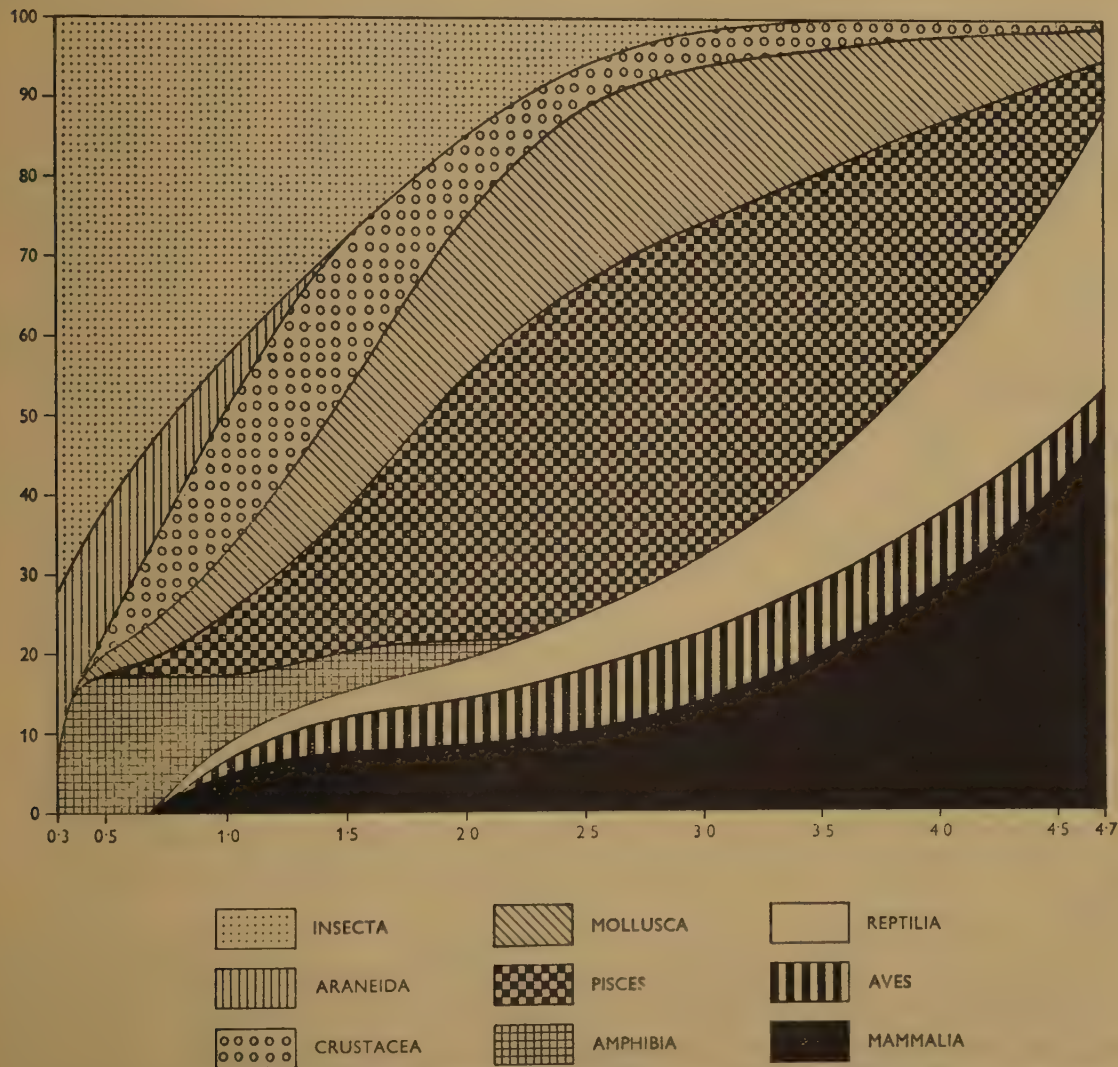


Fig. 35. Generalized diagram showing the progressive changes in feeding habits which accompany growth. The smoothed curves are based upon the number of occurrences, in crocodiles of each half-metre length group, of different foods, expressed as a percentage of the occurrences of all foods.

Quantity of food eaten

It is commonly stated, or assumed, that crocodiles are voracious feeders, daily consuming enormous quantities of fish and other prey. Such notions are quite unsupported by evidence. Indeed, stomach examinations have shown that a large meal is a rarity.

Four repletion categories are here recognized : (i) stomachs empty, except for stones ; (ii) those which contained fragmentary, but recognizable remains of prey—such as insect wings or elytra, gastropod opercula, fish scales, horny chelonian shields, feathers, hair, or claws ; (iii) those which were from a quarter to half full ; and (iv) those which were about three-quarters full and including a few fully-distended stomachs. These quantitative data are analysed, in relation to crocodile Length-Groups, in Table 20.

TABLE 20

Bulk of food in the stomachs of crocodiles of different length-groups.

<i>Length in metres</i>	<i>No. of records</i>	<i>Empty</i>	<i>Fragments only</i>	$\frac{1}{4}$ – $\frac{1}{2}$ <i>full</i>	$\frac{3}{4}$ – <i>full</i>
0–1	138	7 (5·1%)	46 (33·3%)	61 (44·2%)	24 (17·4%)
1–2	190	25 (13·2%)	84 (44·2%)	67 (35·3%)	14 (7·4%)
2–3	164	31 (18·9%)	68 (41·5%)	55 (33·6%)	10 (6·1%)
3–4	89	18 (20·2%)	22 (24·7%)	42 (47·2%)	7 (7·9%)
4–5	10	2 (20·0%)	3 (30·0%)	4 (40·0%)	1 (10·0%)

Of 591 stomachs (from all length groups) only fifty-six (9·5 per cent.) were near repletion ; eighty-three (14·1 per cent.) were empty ; and more than half of the total were either empty or contained indigestible fragments only. Data for the various length groups suggest that in relation to their capacity, young crocodiles feed more actively than their elders. Thus it is in Length Group I that we find the highest proportion of full stomachs (17·4 per cent.); while conversely the percentage with empty stomachs tends to increase with age—from 5·1 in Length Group I to 20·0 in Length Group V.

Analysis of the data, by localities, calls for brief comment. Among ninety-eight Luangwa stomachs, only four were nearly full. Of 369 stomachs examined from Luangwa (98), Kafue (92) and Upper Zambesi (179), 63·2, 56·6 and 60·9 per cent., respectively, were either empty or contained fragments only. Crocodiles from Mweru Wa Ntipa (51) show the lowest percentage of full stomachs (3·9) for any locality, and also the highest percentage (27·5) containing no trace of food.

Crocodiles are usually credited with extraordinary powers of digestion, and to this has been attributed the frequency of empty stomachs. This is contrary to evidence. For example, the stomach of a specimen killed in captivity at Jinja still contained partly digested remains of a small crocodile it had eaten a week previously (Cott, 1954 a). Thus the relative scarcity of food recovered appears to indicate infrequent feeding rather than rapid digestion.

More than half the specimens examined (i.e. categories i and ii) had probably

not taken a large meal for at least a week, although they were shot in waters where fish and other prey abounded. In short, it seems clear that the Nile Crocodile leads an idle life, expending little energy in an environment ideal for a large poikilotherm, and troubles to take only the little food it needs. The field observations suggest that adults take, in bulk, not more than fifty full meals in a year.

These conclusions find support from what is known of the food requirements in captivity. For example, Dr H. G. Vevers tells me (25.5.54) that two crocodiles in the Society's Gardens, each measuring about 2·3 metres, consumed the following rations over an observation period of thirty-six days (16th February to 23rd March) :

(a) Food	Weight in g.	(b) Food	Weight in g.
20 Whiting	4,120	17 Whiting	3,420
7 Rats	700	5 Rats	500
Meat	8,300	Meat	6,200
Total	13,120	Total	10,120

The average daily intake is thus shown to be only about 365 and 280 grams respectively. These crocodiles were not weighed : but specimens of the same length are known, from field measurements, to weigh about 45 kg. These two animals would therefore take, respectively, about 124 and 160 days to consume their own weight of food.

Such slight requirements appear the more striking when compared with the food eaten by waterfowl in nature. For example, stomach examinations of *Pelecanus onocrotalus* in Uganda have shown that a pelican takes at least 6 lbs. (or 2·8 kg.) of fish daily, and may carry prey amounting to one third of its body weight.

Prey of the Nile Crocodile

So far as possible, prey recovered from stomachs has been identified, and the results are tabulated below (Table 21) to afford a comparison between feeding habits in different waters.

Insecta

Insect prey are represented numerically as follows : Coleoptera, 577 ; Hemiptera, 208 ; Odonata, 74 ; Orthoptera, 57 ; Hymenoptera, 44 ; Diptera, 17 ; Dermaptera, 2 ; Lepidoptera, 1. The distribution by families, of prey belonging to the first five orders, is given below :—

COLEOPTERA			HEMIPTERA			ODONATA		
Cicindelidae	29		Hydrometridae	37		Gomphidae	28	
Carabidae	87		Reduviidae	1		Corduliidae	1	
Dytiscidae	54		Belostomatidae	84		Libellulidae	27	
Gyrinidae	2		Naucoridae	72		Agrionidae	1	
Hydrophilidae	93		Nepidae	9				
Tenebrionidae	8		Corixidae	1				
Scarabaeidae	70							
Cerambycidae	1		HYMENOPTERA			ORTHOPTERA		
Curculionidae	1		Apidae	2		Blattidae	1	
			Formicidae	41		Acridiidae	6	
						Tettigoniidae	11	
						Gryllidae	3	
						Gryllotalpidae	31	

TABLE 21

Food of the Nile Crocodile: showing the number of stomachs in which each food was found, and (in italics) the total number of each food organism.

	Uganda (a)*	Uganda (b)*	Bangweulu	Mweru and Kalungwishi	Luangwa	Kafue	Zambesi	Zululand
INSECTA								
ORTHOPTERA								
Blattidae								
Indet.	—	1 1	—	—	—	—	—	—
Acridiidae								
<i>Schistocerca gregaria</i> Forskal	—	—	1 1	—	—	—	—	—
<i>Ornithacris cyanea</i> Stoll	—	—	—	—	—	—	1 1	—
<i>Paracinema tricolor</i> (Thunberg) ..	—	—	—	—	—	2 2	—	—
<i>Trilophidia</i> sp.	—	1 1	—	—	—	—	—	—
Indet.	—	—	—	—	—	1 1	—	—
Tettigoniidae								
<i>Conocephalus conocephalus</i> (Linn.) ..	1 1	—	—	—	—	—	—	—
? <i>Homorocoryphus nitidulus</i> (Scop.) ..	—	—	—	—	—	1 1	—	—
<i>Pseudorhynchus</i> sp.	—	—	—	—	—	—	3 3	—
Indet.	1 1	—	—	—	2 2	1 1	2 2	—
Gryllidae								
<i>Brachytrypes membranaceus</i> (Drury) ..	—	—	—	—	1 1	—	—	—
<i>Paraloxoblemmus angulifrons</i> Chop. ..	1 1	—	—	—	—	—	—	—
Indet.	—	—	—	—	—	—	1 1	—
Gryllotalpidae								
<i>Gryllotalpa africana</i> (Beauv.)	—	1 1	—	1 1	13 26	1 1	1 1	—
Indet.	—	—	1 1	—	—	—	—	—
Orthoptera indet.	1 1	—	2 2	—	—	—	2 2	—
DERMAPTERA								
Labiduridae								
<i>Labidura riparia</i> Pall.	—	1 1	—	—	—	—	—	—
Forficulidae								
<i>Forficula</i> sp.	—	—	—	—	—	1 1	—	—
ISOPTERA								
Termitidae								
<i>Macrotermes bellicosus</i> (Smeathman) ..	2 14	—	—	—	—	—	—	—
ODONATA								
Gomphidae								
<i>Phyllogomphus aethiops</i> Selys	1 1	—	—	—	—	—	—	—
<i>Ictinogomphus ferox</i> Rambur	6 8	4 10	—	—	—	—	3 4	—
<i>Phyllogomphus</i> sp.	—	—	—	—	—	—	2 4	—
Indet.	—	—	—	—	—	—	1 1	—
Corduliidae								
<i>Phyllomacromia picta</i> Selys	1 1	—	—	—	—	—	—	—
Libellulidae								
<i>Brachythemis leucosticta</i> (Burm.) ..	3 3	4 5	—	—	—	—	—	—
<i>Sympetrum navasi</i> Lacroix	1 2	—	—	—	—	—	—	—
<i>Trimethis annulata</i> (Beauv.)	1 1	1 1	—	—	—	—	—	—
<i>Trimethis</i> sp.	1 1	—	—	—	—	—	—	—
<i>Urothemis edwardsi</i> Selys	3 3	—	—	—	—	—	—	—
Indet.	2 11	—	—	—	—	—	—	—

*(a) above Murchison ; (b) below Murchison.

(continued next page)

Table 21—*continuation*

	Uganda (a)	Uganda (b)	Bangweulu	Mweru and Kalungwishi	Luangwa	Kafue	Zambesi	Zululand
Agrionidae								
<i>Ceriagrion</i> sp.	—	—	1 1	—	—	—	—	—
Odonata indet.	4 10	1 1	2 2	—	1 1	1 1	2 2	—
HEMIPTERA								
Gerridae								
<i>Limnogonus hypoleucus</i> (Gerst) ..	2 16	—	—	—	—	1 1	—	—
<i>Limnogonus</i> sp.	—	—	1 20	—	—	—	—	—
Reduviidae								
? <i>Serthenea</i> sp.	—	—	—	—	1 1	—	—	—
Belostomatidae								
<i>Hydrocyrius columbiae</i> Spin.	9 11	1 1	2 2	—	—	3 3	1 1	—
<i>Hydrocyrius</i> sp.	—	—	1 1	—	—	—	—	—
<i>Lethocerus niloticum</i> Stal.	—	—	—	—	2 2	—	—	—
<i>Lethocerus</i> sp.	1 1	1 1	—	—	—	—	—	—
<i>Limnogeton fieberi</i> Mayr	8 15	—	—	—	—	—	—	—
<i>Poissonia longifemorata</i> Brown ..	—	—	4 5	—	—	—	—	—
Indet.	15 22	—	4 6	—	3 3	4 4	5 5	—
Naucoridae								
<i>Laccocoris limigenus</i> Stal.	—	—	—	—	1 1	—	—	—
<i>Sphaerodema ampliatus</i> Bergr. ..	—	—	—	—	1 1	4 6	—	—
<i>Sphaerodema nepoides</i> F.	10 23	2 5	—	—	1 1	2 2	—	—
<i>Sphaerodema</i> sp.	7 20	2 3	6 6	—	1 1	—	3 3	—
Nepidae								
<i>Laccotrephes ater</i> Linn.	—	—	—	—	2 3	1 1	—	—
<i>Ranatra ? nodiceps</i> Gerst.	1 1	—	—	—	—	2 2	—	—
<i>Ranatra</i> sp.	1 1	1 1	—	—	—	—	—	—
Corixidae								
Indet.	—	1 1	—	—	—	—	—	—
Hemiptera indet.	1 1	—	1 3	—	—	—	—	—
LEPIDOPTERA								
Noctuidae								
Larva indet.	1 1	—	—	—	—	—	—	—
COLEOPTERA								
Cicindelidae								
<i>Cicindela dongalensis</i> Klug.	—	—	—	—	8 29	—	—	—
Carabidae								
<i>Scarites aestuans</i> Klug	—	—	—	—	13 34	—	4 10	—
<i>Scarites</i> sp.	—	—	1 1	1 1	2 3	—	2 4	—
<i>Eudema</i> sp.	—	—	—	—	1 1	—	1 1	—
<i>Chlaenius ? circumscriptus</i> Dej. ..	—	—	—	—	1 2	—	—	—
<i>Chlaenius</i> sp.	—	—	—	—	2 3	—	—	—
<i>Macrochlaenites lugens</i> Chaud. ..	—	—	—	2 6	—	—	—	—
<i>Cyclosomus equestris</i> Boh.	—	1 6	—	—	—	—	—	—
<i>Pheropsophus transvaalensis</i> Pér. ..	—	—	—	—	2 2	—	—	—
<i>Pheropsophus ? kersteni</i> Gerst. ..	1 1	—	—	—	—	—	—	—
<i>Pheropsophus</i> sp.	2 7	—	—	—	—	—	1 1	—
Indet.	1 2	—	—	—	2 2	—	—	—

(continued next page)

Table 21—*continuation*

				Uganda (a)	Uganda (b)	Bangweulu	Mweru and Kalungwishi	Luangwa	Kafue	Zambesi	Zululand
Dytiscidae											
<i>Hydaticus dorsiger</i> Aubé	—	—	—	1 1	—	—	—	—
<i>Hydrocanthus</i> sp.	—	3 11	—	—	—	—	—	—
<i>Hydrovatus frater</i> Rég.	—	1 1	—	—	—	—	—	—
<i>Regimbartia</i> ? <i>nilotica</i> Sap.	—	3 12	—	—	—	—	—	—
<i>Cybister binotatus</i> Klug	—	—	—	—	—	—	1 1	—
<i>Cybister</i> ? <i>natalensis</i> Whn.	—	—	—	—	—	2 5	—	—
<i>Cybister senegalensis</i> Aubé	—	—	2 2	—	—	—	—	—
<i>Cybister</i> ? <i>tripunctatus</i> Cast.	—	—	1 1	—	1 1	—	—	—
<i>Cybister vicinus</i> Zimm.	—	—	—	—	1 1	—	—	—
<i>Cybister</i> sp.	2 2	3 3	1 1	—	—	3 3	5 9	—
Gyrinidae											
<i>Orectogyrus</i> sp.	—	1 1	—	—	—	—	—	—
Indet.	—	1 1	—	—	—	—	—	—
Hydrophilidae											
<i>Coelostoma</i> sp.	1 7	1 2	—	—	—	—	—	—
<i>Helochares</i> sp.	—	1 1	—	—	—	—	—	—
<i>Sternolophus angolensis</i> Cast.	—	—	—	—	—	—	1 1	—
<i>Sternolophus</i> sp.	—	—	2 2	—	—	—	—	—
<i>Hydrophilus aculeatus</i> Sol.	—	—	—	—	1 1	25 54	11 14	—
<i>Hydrophilus marginatus</i> Lap.	—	—	1 2	—	—	—	—	—
<i>Hydrophilus</i> sp.	—	—	1 3	—	—	—	1 1	—
<i>Hydrochara</i> sp.	—	—	1 1	—	—	—	—	—
<i>Amphiops senegalensis</i> Cast.	—	2 3	—	—	—	—	—	—
<i>Allocotocerus</i> sp.	—	1 1	—	—	—	—	—	—
Tenebrionidae											
<i>Adesmia</i> sp.	—	—	—	1 1	—	—	—	—
<i>Macropoda</i> sp.	—	—	—	1 1	—	—	—	—
<i>Peristepus</i> sp.	—	—	—	—	1 1	—	—	—
<i>Gonocephalum simplex</i> F.	1 1	—	—	—	—	—	—	—
<i>Achrostus</i> sp.	1 1	—	—	—	—	—	—	—
Indet.	—	2 3	—	—	—	—	—	—
Scarabaeidae											
<i>Helicopris</i> ? <i>colossus</i> Bates	1 1	1 1	—	—	—	—	—	—
<i>Heteroligus</i> ? <i>gazanus</i> Arrow	—	—	—	—	—	—	1 1	—
<i>Heteroligus meles</i> Billb.	—	—	—	—	1 8	—	—	—
<i>Heteronychus pauperatus</i> Pér.	—	—	—	—	—	1 2	—	—
<i>Heteronychus wilmsi</i> Kolbe	—	—	—	—	—	—	1 1	—
<i>Heteronychus</i> sp.	—	—	2 3	1 1	—	10 20	4 4	—
<i>Temnorhynchus coronatus</i> F.	—	—	—	—	6 6	—	1 1	—
<i>Temnorhynchus elongatus</i> Arrow	—	—	—	—	—	—	1 1	—
<i>Temnorhynchus</i> sp.	—	—	—	—	8 13	—	2 3	—
Indet.	—	1 1	—	—	—	—	3 3	—
Cerambycidae											
Indet.	1 1	—	—	—	—	—	—	—
Curculionidae											
Indet.	—	—	—	1 1	—	—	—	—
Coleoptera indet.	1 3	4 18	4 40	1 1	29 65	21 43	36 62	—
HYMENOPTERA											
Apidae											
<i>Apis mellifera</i> Linn.	1 2	—	—	—	—	—	—	—

(continued next page)

Table 21—*continuation*

	Uganda (a)	Uganda (b)	Banquetula	Mweru and Kalungwishi	Luangwa	Kafue	Zambesi	Zululand
Formicidae								
<i>Bothroponera</i> sp.	—	1 1	—	—	—	—	—	—
<i>Odontomachus assiniensis</i> Emery	2 9	—	—	—	—	—	—	—
<i>Paltothyreus tarsatus</i> Fab.	1 4	—	—	—	—	—	—	—
<i>Psolidomyrmex</i> sp.	1 1	—	—	—	—	—	—	—
<i>Euponera</i> sp.	1 1	—	—	—	—	—	—	—
<i>Camponotus</i> sp.	3 10	—	—	—	—	—	—	—
<i>Myrmecaria</i> sp.	1 4	—	—	—	—	—	—	—
<i>Dorylus</i> sp.	—	—	—	—	1 1	—	1 1	—
Indet.	2 3	1 4	—	—	3 3	—	—	—
DIPTERA								
Tachinidae								
<i>Sturmia</i> sp.	1 2	—	—	—	—	—	—	—
Otitidae								
Indet.	1 1	—	—	—	—	—	—	—
Anthomyidae								
Indet.	1 1	—	—	—	—	—	—	—
Diptera indet.	—	—	—	—	—	—	1 1	—
Insecta indet.	5 7	1 1	1 2	—	2 2	—	—	—
ARACHNIDA								
ARANEIDA								
Tetragnathidae								
<i>Tetragnatha</i> sp.	—	—	—	—	—	—	1 2	—
Pisauridae								
<i>Dolomedes bistylus</i> Roewer	—	—	—	—	—	1 1	1 1	—
<i>Dolomedes lesserti</i> Roewer	—	—	—	—	—	2 2	2 2	—
<i>Dolomedes</i> sp.	—	—	1 1	1 4	—	1 2	1 1	—
<i>Thalassius</i> sp.	—	—	—	—	—	—	2 4	—
Araneida indet.	5 6	5 8	—	1 1	1 1	2 2	4 6	—
CRUSTACEA								
BRACHYURA								
Potamonidae								
<i>Potamonautes niloticus</i> (M.-Edw.)	5 6	—	—	—	—	—	—	—
<i>Potamonautes ? bayonianus</i> (Capello)	—	—	—	—	—	—	48 56	—
<i>Potamonautes</i> sp.	11 13	—	2 2	—	—	23 32	18 28	—
MACRURA								
Atyidae								
<i>Caridina nilotica</i> de Man	1 1	—	—	—	—	—	—	—
<i>Caridina</i> sp.	—	1 1	—	—	—	—	—	—
MOLLUSCA								
GASTROPODA								
Ampulariidae								
<i>Pila ovata</i> (Olivier)	5 60	—	—	—	—	—	—	—
<i>Lanistes ovum</i> Peters	—	—	20 1155	13 528	6 21	26 1610	20 82	—
Viviparidae								
<i>Bellamya unicolor</i> Olivier	1 8	—	—	—	—	—	—	—
Hydrobiidae								
<i>Gabbia tilhoi</i> Germain	—	1 1	—	—	—	—	—	—

(continued next page)

Table 21—*continuation*

		Uganda (a)	Uganda (b)	Bangweulu	Mweru and Katangwishu	Luangua	Kafue	Zambesi	Zululand
PULMONATA									
Planorbidae									
<i>Biomphalaria choanomphala</i> V. Martens		—	1 1	—	—	—	—	—	—
<i>Biomphalaria sudanica</i> V. Martens ..		1 1	1 4	—	—	—	—	—	—
<i>Segmentina angusta</i> Limnaeidae ..		—	1 1	—	—	—	—	—	—
Limnaeidae									
<i>Limnaea natalensis</i> Krauss		—	—	—	—	—	2 2	—	—
Gastropoda indet.		6 7	—	29 627	—	—	2 5	10 78	—
LAMELLIBRANCHIATA									
Sphaeriidae									
<i>Sphaerium</i> sp.		—	1 1	—	—	—	—	—	—
Unionidae									
<i>Parreyssia</i> ? <i>kunensis</i> Mouss		—	—	—	—	—	1 1	—	—
Lamellibranchiata indet.		—	—	—	—	—	3 3	2 2	—
CHONDRICHTHYES									
SELACHII									
Shark, indet.		—	—	—	—	—	—	—	1 2
OSTEICHTHYES									
DIPNOI									
Lepidosirenidae									
<i>Protopterus aethiopicus</i> Heckel		7 7	—	—	—	—	—	—	—
ISOSPONDYLI									
Mormyridae									
<i>Mormyrus caschive</i> Linn.		—	1 1	—	—	—	—	—	—
<i>Mormyrus</i> sp.		3 11	—	—	—	—	—	—	—
<i>Gnathonemus montei</i> Blgr.		—	—	1 1	—	—	—	—	—
<i>Gnathonemus macrolepidotus</i> Peters ..		—	—	—	—	—	—	1 4	—
Indet.		—	—	—	—	—	—	1 1	—
OSTARIOPHYSI									
Characidae									
<i>Hydrocyon lineatus</i> Blgr.		—	—	1 1	—	—	—	—	—
<i>Hydrocyon</i> ? <i>vittatus</i> (Cast.)		—	—	—	—	2 2	—	1 3	—
<i>Hydrocyon</i> sp.		—	2 3	1 1	—	—	—	1 1	—
<i>Hepsetus odoë</i> (Bloch)		—	—	—	—	—	2 2	—	—
<i>Alestes macrophthalmus</i> Gunth.		—	—	—	1 4	—	—	—	—
<i>Alestes</i> sp.		—	2 10	—	—	—	—	—	—
Cyprinidae									
<i>Barbus bynni</i> Forsk.		—	1 1	—	—	—	—	—	—
<i>Barbus eutaenia</i> Blgr.		—	—	—	—	—	1 1	—	—
<i>Barbus radcliffii</i> Blgr.		3 3	—	—	—	—	—	—	—
<i>Barbus</i> sp.		1 1	—	—	—	—	—	—	—
<i>Labeo</i> sp.		—	1 2	—	—	—	—	—	—
Bagridae									
<i>Auchenoglanis occidentalis</i> C. & V. ..		—	3 8	—	—	—	—	—	—

(continued next page)

Table 21—continuation

	Uganda (a)	Uganda (b)	Bangweulu	Mweru and Kalangwishi	Luangwa	Kafue	Zambesi	Zululand
Schilbeidae								
<i>Schilbe</i> ? <i>mystus</i> Linn.	—	—	1 1	—	—	—	—	—
<i>Eutropius bangweulensis</i> Blgr.	—	—	1 2	—	—	—	—	—
Clariidae								
<i>Clarias mossambicus</i> Peters	—	—	—	29 42	—	1 1	2 2	—
<i>Clarias</i> ? <i>mellandi</i> Blgr.	—	—	—	—	—	2 2	—	—
<i>Clarias</i> sp.	—	1 1	1 1	1 1	—	3 3	28 34	—
Mochocidae								
<i>Synodontis schall</i> Bl.-Schn.	—	1 4	—	—	—	—	—	—
<i>Synodontis frontosus</i> Vaill.	—	1 1	—	—	—	—	—	—
<i>Synodontis nigromaculatus</i> Blgr.	—	—	2 2	—	—	—	—	—
<i>Synodontis zambesensis</i> Peters	—	—	—	—	1 1	—	5 6	—
<i>Synodontis</i> sp.	—	2 7	2 2	—	—	—	11 11	—
Siluroidea indet.	—	—	—	—	2 2	2 2	—	1 1
APODES								
Anguillidae								
Indet.	—	—	—	—	—	—	—	1 1
MICROCYPRI								
Cyprinodontidae								
<i>Aplocheilichthys</i> sp.	—	—	—	—	—	1 1	—	—
PERCOMORPHI								
Plectorhynchidae								
<i>Pomadasys operculare</i> (Playf.)	—	—	—	—	—	—	—	1 6
Centropomidae								
<i>Lates</i> sp.	—	1 1	—	—	—	—	—	—
Cichlidae								
<i>Tilapia macrochir</i> Blgr.	—	—	1 1	—	—	—	—	—
<i>Tilapia sparrmani</i> A. Smith	—	—	1 2	—	—	—	—	—
<i>Tilapia andersonii</i> Cast.	—	—	—	—	—	1 1	2 2	—
<i>Tilapia mossambicus</i> Peters	—	—	—	—	1 1	—	—	—
<i>Tilapia melanopleura</i> Dumeril	—	—	—	—	—	—	2 2	—
<i>Tilapia</i> sp.	1 1	2 2	2 4	—	—	3 5	13 15	1 1
<i>Serranochromis angusticeps</i> (Blgr.)	—	—	1 2	—	—	—	—	—
<i>Serranochromis thumbergii</i> (Cast.)	—	—	—	—	—	—	2 2	—
<i>Serranochromis</i> sp.	—	—	—	—	—	—	1 1	—
<i>Sargochromis codringtoni</i> Blgr.	—	—	—	—	—	—	1 1	—
<i>Sargochromis mellandi</i> (Blgr.)	—	—	1 1	—	—	—	—	—
<i>Astatoreochromis alluaudi</i> Pellegrin	1 1	—	—	—	—	—	—	—
<i>Haplochromis moffattii</i> (Cast.)	—	—	—	—	—	2 4	—	—
<i>Haplochromis darlingi</i> Blgr.	—	—	—	—	—	—	1 1	—
<i>Haplochromis</i> sp.	1 1	—	—	—	—	1 1	1 1	—
Indet.	—	—	—	—	1 2	1 1	2 2	—
Pisces indet.	13 13	1 2	32 52	3 3	1 1	18 21	30 30	5 5
AMPHIBIA								
ANURA								
Bufonidae								
<i>Bufo regularis</i> Reuss	1 3	—	—	—	6 9	—	1 1	—
<i>Bufo</i> sp.	1 1	—	1 1	—	2 2	—	—	—

(continued next page)

Table 21—*continuation*

					Uganda (a)	Uganda (b)	Bangweulu	Mweru and Kalungwishi	Luangwa	Kafue	Zambesi	Zululand
Ranidae												
<i>Arthroleptis</i> sp.	—	—	1 1	—	—	—	—	—
<i>Phrynobatrachus natalensis</i> (Smith)	—	—	—	—	1 1	—	—	—
Polypedatidae												
<i>Hyperolius</i> sp.	5 6	—	—	—	—	—	—	—
Brevicipitidae												
<i>Hemisus marmoratum</i> (Peters)	—	—	—	—	1 1	—	—	—
<i>Anura</i> indet.	8 16	1 1	1 1	—	6 7	2 4	3 5	—
REPTILIA												
CHELONIA												
Pelomedusidae												
<i>Pelusios subniger</i> (Lacépède)	—	3 3	—	1 1	2 2	2 3	7 7	—
<i>Pelusios sinuatus</i> (Smith)	—	—	—	—	1 1	—	—	—
<i>Pelusios</i> sp.	—	—	—	—	—	4 4	3 3	—
Indet.	—	—	—	—	—	—	6 6	5 5
CROCODYLIA												
Crocodilidae												
<i>Crocodilus niloticus</i> Blgr.	9 9	1 1	—	3 3	2 2	—	2 2	1 1
Eggs	—	—	—	—	—	—	—	1 82
LACERTILIA												
Varanidae												
<i>Varanus niloticus</i> (Linn.)	—	1 1	—	—	3 3	1 1	3 3	1 1
OPHIDIA												
Boidae												
<i>Python sebae</i> (Gmelin)	—	—	1 1	—	—	—	1 1	—
Colubridae												
<i>Natrix olivacea</i> (Peters)	2 2	—	—	—	—	—	—	—
<i>Boaedon lineatum</i> (Dum. & Bib.)	—	—	—	—	1 1	—	—	—
<i>Chlorophis hoplogaster</i> (Günther)	—	—	—	—	—	4 4	—	—
<i>Dasypeltis scabra</i> (Linn.)	1 1	—	—	—	—	—	—	—
<i>Naia melanoleuca</i> Hallowell	1 1	—	—	—	—	—	—	—
Viperidae												
<i>Bitis arietans</i> (Merrem)	—	—	—	—	—	1 1	—	—
Ophidia indet.	—	—	1 1	—	2 2	1 1	—	—
AVES												
PELECANIFORMES												
Phalacrocoracidae												
<i>Phalacrocorax lucidus</i> (Licht.)	1 1	—	—	—	—	—	—	—
<i>Phalacrocorax africanus</i> (Gmel.)	—	—	2 2	—	—	2 3	—	—
<i>Phalacrocorax</i> sp.	2 2	—	—	—	—	1 1	6 6	—
Anhingidae												
<i>Anhinga rufa</i> (Lacépède & Daudin)	2 2	—	—	—	2 2	2 2	1 1	—
Pelecanidae												
? <i>Pelecanus</i> sp.	—	—	—	—	—	1 1	—	—
Pelecaniformes indet.	1 1	—	—	—	—	—	—	—

(continued next page)

Table 21—*continuation*

	Uganda (a)	Uganda (b)	Banqueula	Mweru and Kalungwishi	Luangwa	Kafue	Zambesi	Zululand
CICONIIFORMES								
Ardeidae								
<i>Ardea purpurea</i> Linn.	—	—	—	—	—	—	1 1	—
ANSERIFORMES								
Anseridae								
? <i>Anas sparsa</i> Eyton	—	—	—	—	—	—	1 1	—
<i>Anas undulata</i> Dubois	—	—	1 1	—	—	—	—	—
? <i>Sarkidiornis melanota</i> (Pennant) ..	—	—	—	1 1	—	—	—	—
Indet.	—	—	2 2	—	—	—	—	3 4
RALLIFORMES								
Rallidae								
<i>Porphyryla alleni</i> (Thomson)	—	—	—	1 1	—	—	—	—
<i>Porphyrio alba</i> (White)	—	—	—	—	—	1 1	—	—
COLUMBIFORMES								
Columbidae								
? <i>Streptopelia capicola</i> (Sundev.) ..	—	—	—	—	1 1	—	—	—
Indet.	—	—	—	—	1 1	—	—	—
CAPRIMULGIFORMES								
Caprimulgidae								
<i>Caprimulgus fossii</i> Hartlaub	—	—	—	—	—	—	1 1	—
PASSERIFORMES								
Ploceidae								
Estrildine sp.	—	—	—	—	1 1	—	—	—
Indet.	1 1	—	1 1	—	—	—	—	—
Aves indet.	4 4	—	2 2	—	3 3	7 7	5 5	1 2
MAMMALIA								
PHOLIDOTA								
Manidae								
<i>Manis tricuspis</i> Rafinesque	1 1	—	—	—	—	—	—	—
PERISSODACTYLA								
Equidae								
<i>Equus asinus</i> Linn.	—	—	—	—	—	—	—	1 1
<i>Equus burchellii</i> (J. E. Gray)	—	—	—	—	1 1	—	—	—
ARTIODACTYLA								
Hippopotamidae								
<i>Hippopotamus amphibius</i> Linn. ..	1 1	2 2	—	1 1	1 1	—	—	1 1
Suidae								
<i>Potamochoerus porcus</i> Linn.	—	—	—	—	—	—	—	2 2

(continued next page)

Table 21—*continuation*

	Uganda (a)	Uganda (b)	Bangweulu	Mweru and Kalungishi	Luangwa	Kafue	Zambesi	Zululand
Bovidae								
<i>Bos taurus</i> Linn.	—	—	—	—	—	2 2	1 1	3 3
<i>Ovis aries</i> Linn.	—	—	—	—	—	—	—	1 1
<i>Capra hircus</i> Linn.	—	—	—	—	—	—	—	2 2
<i>Redunca arundinum</i> Boddaert	—	—	—	—	—	—	1 1	—
<i>Kobus ellipsiprymnus</i> (Ogilby)	—	1 1	1 1	—	—	1 1	1 1	—
<i>Kobus leche</i> J. E. Gray	—	—	1 1	—	—	2 2	—	—
<i>Hippotragus niger</i> (Harris)	—	—	—	—	—	—	1 1	—
<i>Tragelaphus spekii</i> Sclater	—	—	2 2	—	—	—	1 1	—
? <i>Cephalophus natalensis</i> A. Smith	—	—	—	—	—	—	—	1 1
Indet.	1 1	—	—	1 1	—	1 1	—	—
CARNIVORA								
Canidae								
<i>Canis familiaris</i> Linn.	1 1	—	—	—	—	1 1	2 2	3 3
Mustelidae								
<i>Lutra maculicollis</i> Licht.	—	—	—	1 1	—	—	—	—
Viverridae								
<i>Atilax paludinosus</i> (G. Cuvier)	—	—	2 2	—	—	—	—	—
<i>Genetta</i> sp.	—	—	—	—	1 1	—	—	—
Indet.	—	—	—	—	—	3 3	—	—
RODENTIA								
Hystriidae								
<i>Hystrix africaeaustralis</i> Peters	—	—	—	—	—	—	—	1 1
Octodontidae								
<i>Thryonomys swinderianus</i> (Temmm.)	—	—	2 2	—	8 8	—	4 4	3 5
Muridae								
<i>Mastomys natalensis</i> A. Smith	—	—	—	—	—	—	1 1	—
<i>Dasyms incommis</i> (Sundevall)	—	—	—	—	—	1 1	—	—
<i>Oenomys hypoxanthus</i> Puch	1 1	—	—	—	—	—	—	—
? <i>Otomys</i> sp.	—	—	1 1	—	—	—	—	—
Indet.	—	—	—	—	4 4	—	—	—
Rodentia indet.	3 3	1 1	5 9	—	—	1 1	9 9	—
PRIMATES								
Cercopithecidae								
<i>Papio ursinus</i> Kerr	—	—	—	—	—	—	—	2 2
<i>Cercopithecus</i> sp.	—	—	—	—	—	—	—	2 3
Hominidae								
Human remains	—	—	—	—	—	2 2	1 1	1 1
Mammalia indet.	4 4	1 1	3 3	1 1	4 4	7 7	4 4	—

Coleoptera—making up more than half of the total insect catch—represent the bulk of insects taken by crocodiles in the Luangwa, Kafue and Zambesi Rivers, but not in Uganda and Bangweulu Swamp. As might be expected, water-beetles are well represented—both Hydrophilidae (including various species of *Hydrophilus*) and Dytiscidae (such as the large predaceous *Cybister*) being prominent. But a surprising feature of the collection is the large number of terrestrial forms—notably Carabidae, Scarabaeidae and Cicindelidae. Land-beetles number 196 as

compared with 148 water-beetles : most of the former must have been taken when crocodiles were feeding ashore or climbing in vegetation over shallows.

Hemiptera are well represented from most localities, giant water-bugs (Belostomatidae) being prevalent. Such bugs as *Hydrocyrius*, *Lethocerus* and *Limnogaster* are the largest insects available to crocodiles, and especially in Uganda, they make a substantial food source which juveniles have been ready to exploit.

Orthoptera include both long- and short-horned grasshoppers, crickets and mole-crickets ; but only in the Luangwa Valley can they be regarded as other than incidental captures. Luangwa juveniles had fed quite extensively upon *Gryllotalpa africana*. Orthopterous prey again provide indirect evidence of the terrestrial hunting habits of young crocodiles.

Odonata were mostly taken from stomachs examined in Uganda (58 of 74 specimens). There are only three records from Bangweulu, and only two were found in 303 stomachs containing other food, from the Kafue and Zambesi Rivers. Dr P. S. Corbet (15.6.55) has most kindly examined a sample of the Uganda material. His analysis is as follows :

Larvae, 24 : pharate or exuviae, 23 ; non-pharate, 1.
Adults, 7 : immature, 4 ; mature, 3.

In this sample of thirty-one specimens, at least twenty-seven (87 per cent.) were probably taken at the time of emergence. This suggests that the reptiles must have been taking their prey on, or near to, the shore ; and that—since the species here represented all leave the water prior to emergence soon after dusk—the crocodiles had captured most of their prey at night. Both of these conclusions, for which I am indebted to Corbet, are fully confirmed by field observation.

Araneida

At no time of life do spiders make a substantial contribution to a crocodile's diet. Of forty-four spiders recovered, all but seven were from juveniles less than one metre in length, and none were found in any crocodile over two metres in length. Most of the specimens identified are referable to *Dolomedes*, a genus of water-spiders which frequent floating vegetation, from which they make predatory sorties over the surface film.

Mollusca

One of the surprising facts here brought to light is the quite unexpected role of molluscs in crocodile ecology. Of 673 stomachs containing food of any kind from Uganda and Rhodesia, 145 (21.5 per cent.) contained molluscs. This food is taken by crocodiles of all length groups. In terms of the number of prey, molluscs far exceed all other food organisms, and account for nearly 70 per cent. of the total. Predation upon ampulariid water snails was especially heavy in Bangweulu Swamp, Mweru Wa Ntipa, and the Kafue Flats, where molluscs represent 89.1, 87.0 and 84.7 per cent. of all prey. The very high proportion of Gastropoda (4192) as compared with Lammellibranchiata (only 6) is remarkable. The former consist almost entirely of ampulariids—*Pila ovata*, a species

common on rock surfaces just below water-line, in Uganda ; and *Lanistes ovum*, which is found submerged among water plants and on detritus in Rhodesian waters.

Crustacea

Remains of 137 crabs were recovered from 106 stomachs. The importance of crabs as food varied widely in different waters. None were found in stomachs examined in Bangweulu, Mweru Wa Ntipa, the Kalungwishi River or Luangwa Valley. On the other hand, in the Kafue and especially in the Upper Zambesi, crabs of the genus *Potamonautes* form a substantial element in the diet of crocodiles up to about 1.5 metres in length. In Uganda the prey species is *P. niloticus*, and in Rhodesia, apparently *B. bayonianus*.

Pisces

The percentage occurrence of invertebrates, fish, and other vertebrates throughout the life cycle is summarised in Fig. 36, from which it will be seen that the

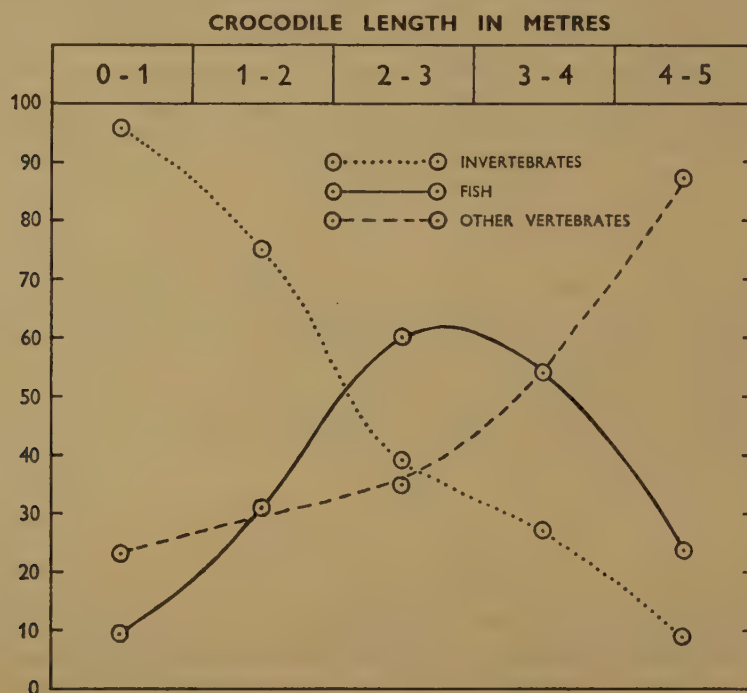


Fig. 36. Changes in the feeding pattern which accompany growth, with special reference to fish prey. Occurrences of three categories of food are expressed as a percentage of stomachs containing food of any kind.

relative importance of fish, as prey, changes markedly with age. It is only in the length range from about 2.0 to 3.5 metres that fish form the main food.

Wholly extravagant views as to the quantity of fish eaten have been held in

the past. For example, Capt R. J. D. Salmon (1932), referring to crocodiles feeding below Murchison Falls, mentions 50 lbs. a night as an estimate. Nothing approaching this weight has been found in any crocodile examined by me. Remains of some 393 fish were recovered from 265 of the 851 crocodiles examined. In 701 stomachs containing food of any kind, the percentage occurrence of fish-prey is 37·8 ; and the number of fish per stomach only 0·56.

The proportions in which various genera are taken varies markedly according to locality. On Lakes Kioga and Kwania it appears from Hippel's investigation (1946) that *Protopterus* and *Barbus* together account for nearly two-thirds of the catch, the remaining genera, in order of importance, comprising *Tilapia*, *Clarias*, *Bagrus*, *Mormyrus* and *Haplochromis*. My own data from waters in Uganda above Murchison Falls agree in placing *Protopterus* and *Barbus* as the main prey (some of my *Mormyrus* records were from crocodiles that had been feeding on offal discarded near fish-camps).

The records from the Semliki River, Lake Albert and the Nile below Murchison indicate that *Synodontis*, *Alestes*, and *Auchenoglanis* are most frequently taken (in the order given).

Lake Bangweulu in Northern Rhodesia was the only locality in which catches of *Tilapia* were in excess of any other genera (seven specimens among a total of twenty-one fish identified). In Mweru Wa Ntipa crocodiles were feeding almost entirely upon *Clarias*. Prey records from the Upper Zambesi and Kafue include the following genera as most frequent : *Clarias*, 42 ; *Tilapia*, 25 ; *Synodontis*, 17 ; *Haplochromis* and allied genera, 14.

Amphibia

Frogs and toads are eaten during the first three or four years of life (up to 1·5 metres in length). Thereafter this prey almost disappears from the diet and no Anura were recorded from any crocodile exceeding 2·5 metres. The species most frequently taken, both in Uganda and Northern Rhodesia, is *Bufo regularis*.

Reptilia

Reptiles or their remains were found in seventy-seven stomachs, as follows : Ophidia, 16 ; Lacertilia, 9 ; Chelonia, 35 ; Crocodilia, 17. Most of the snakes were small riverine species such as *Natrix olivacea* and *Chlorophis hoplogaster* which could have been taken in the water : this also applies to a large Black Cobra (*Naja melanoleuca*) taken at Fajao. A surprising catch was a Puff Adder (*Bitis arietans*) from the Kafue Flats. Two crocodiles had eaten African Python (*Python sebae*). Three snakes were recovered from juveniles less than a metre in length, these being the smallest crocodiles to contain reptilian prey of any kind.

The Nile Monitor (*V. niloticus*)—the only species of lizard identified—is doubtless preyed upon in all localities where it associates with crocodiles, present records including Murchison (1), Luangwa (3), Kafue (1), Zambesi (3), Zululand (1). Most

of the identified turtles were *Pelusios subniger*, a species very common in the muddy waters of the Kafue and Zambesi.

Cannibalism

Crocodiles are much addicted to cannibalism and this is doubtless one of the factors which accounts for their segregation in "age-groups" on the basking grounds and elsewhere. Evidence of cannibalism is afforded by (i) injured specimens, (ii) direct observations, and (iii) stomach contents. Injuries that may be attributed to cannibalistic assaults are not infrequent. Predatory attacks by one crocodile upon another have rarely been witnessed, though these are known to occur in captivity. Wajalubi told me (1952) that he had seen an old crocodile prey upon a young one in the Semliki River; and both Pitman (1935) and Poles (1956) give details of such attacks. But the main evidence is to be derived from stomach examinations. In 1952 N. H. Searle recovered a crocodile's tail from the stomach of another individual. In Zululand, P. H. Jackson found a crocodile measuring about one metre in the stomach of another four metres in length. In Uganda Hippel (1946) found crocodile remains in thirty-seven of 587 crocodiles examined; and he ascertained that these could not derive from carcasses caught by his organization. Of the seventeen occurrences of crocodile prey now recorded (Uganda 9, Mweru 3, Luangwa 2, Zambesi 2, Zululand 1) only two of the predators (both from Luangwa) measured less than 3 metres, and no fewer than eight were very large, ranging from 4.1 to 4.9 metres. Cannibalism thus appears to be a habit acquired with age.

Aves

Birds are preyed upon by crocodiles of all length groups, and the records show a more even distribution for avian than for any other type of prey. But at no period do they form an important food. Bird remains were found in sixty of 701 stomachs containing food of any kind. These figures are in general agreement with Hippel's recoveries of bird remains from thirty-eight of 587 stomachs (Hippel, 1946)—the percentage occurrence for the two series of observations being 8.6 and 6.5 respectively.

Much of the present material was too fragmentary for identification. So far as determination allows of analysis, the several orders are represented by specimens as follows: Pelecaniformes, 24; Anseriformes, 9; Passeriformes, 3; Ralliformes, 2; Columbiformes, 2; Ciconiiformes, 1; Caprimulgiformes, 1.

African records from many sources have been collected by Pitman (1957). While it is known that a very wide range of birds may be taken by the Nile Crocodile—from pelicans and Fish Eagle to weavers and swallows—it now seems clear that cormorants (*Phalacrocorax lucidus* and *P. africanus*) and darters (*Anhinga rufa*) make up the bulk of captures.

Mammalia

The frequency of occurrence of mammals rises with growth of the predator.

Various mammalian orders represented in the present material are as follows : Rodentia, 51 ; Artiodactyla, 33 ; Carnivora, 13 ; Primates, 9 ; Perissodactyla, 2 ; Pholidota, 1. Nearly half of the identified specimens were rodents ; much hair listed in Table 21 as unidentified was certainly of rodent origin and seemed to be either *Dasymys*, *Otomys*, *Pelomys* or *Arvicanthis* (Ansell, 4.9.57). In Northern Rhodesia and Zululand the Cane Rat (*Thryonomys swinderianus*) is numerically the most important prey species.

Attacks upon game animals do not appear to be heavy, except perhaps in the Kafue near Lochinvar Ranch. From the whole series under review, remains of antelopes were found in sixteen of 323 stomachs of crocodiles larger than 2.0 metres, as follows : Waterbuck, 4 ; Lechwe, 3 ; Situtunga, 3 ; Sable, 1 ; Reedbuck, 1 ; Natal Duiker, 1 ; unidentified, 3. Evidence of predation upon domestic cattle was found in six stomachs, and of sheep or goats in three stomachs. The records from all areas also include six hippopotamus, and four human fatalities.

Food in relation to locality

Considerable differences have been found in the proportions and kinds of prey taken in different localities. Tables 22 to 27 give comparative data for the main categories. In these tables the occurrences are expressed, under each Length Group, as a percentage of stomachs containing food of any kind. Since many stomachs contained more than one kind of food, it has been necessary to adjust percentages in the comparative histograms (Fig. 37), where the occurrence of a particular food is expressed, within each Length Group, as a percentage of all occurrences.

Salient features in the diet of crocodiles in different localities are here briefly summarised.

TABLE 22

Number and percentage of stomachs containing various foods, by Length Groups : Uganda.

<i>Length in metres</i>	<i>0-1</i>	<i>1-2</i>	<i>2-3</i>	<i>3-4</i>	<i>4-5</i>
Number of crocodiles containing prey	49	25	13	19	18
Insecta ..	47 (96.0%)	16 (64.0%)	—	1 (5.3%)	—
Araneida ..	8 (16.3%)	2 (8.0%)	—	—	—
Crustacea ..	3 (6.1%)	11 (44.0%)	2 (15.4%)	—	—
Mollusca ..	4 (8.2%)	5 (20.0%)	3 (23.1%)	2 (10.5%)	—
Pisces ..	2 (4.1%)	10 (40.0%)	12 (92.3%)	15 (79.0%)	5 (27.8%)
Amphibia ..	11 (22.4%)	4 (16.0%)	1 (7.7%)	—	—
Reptilia ..	2 (4.1%)	2 (8.0%)	1 (7.7%)	3 (15.8%)	10 (55.6%)
Aves ..	—	4 (16.0%)	2 (15.4%)	4 (21.1%)	1 (5.6%)
Mammalia ..	2 (4.1%)	3 (12.0%)	2 (15.4%)	2 (10.5%)	7 (38.9%)

TABLE 23
Number and percentage of stomachs containing various foods, by Length Groups : Bangweulu.

<i>Length in metres</i>	<i>0-1</i>	<i>1-2</i>	<i>2-3</i>	<i>3-4</i>
Number of crocodiles containing prey ..	18	28	44	20
Insecta	12 (66.7%)	5 (17.9%)	1 (2.3%)	—
Araneida	1 (5.5%)	—	—	—
Crustacea	1 (5.5%)	1 (3.6%)	—	—
Mollusca	1 (5.5%)	11 (39.3%)	27 (61.4%)	10 (50.0%)
Pisces	5 (27.8%)	14 (50.0%)	17 (38.6%)	8 (40.0%)
Amphibia	1 (5.5%)	1 (3.6%)	—	—
Reptilia	—	—	1 (2.3%)	1 (5.0%)
Aves	2 (11.1%)	1 (3.6%)	3 (6.8%)	2 (10.0%)
Mammalia	—	2 (7.1%)	7 (15.9%)	7 (35.0%)

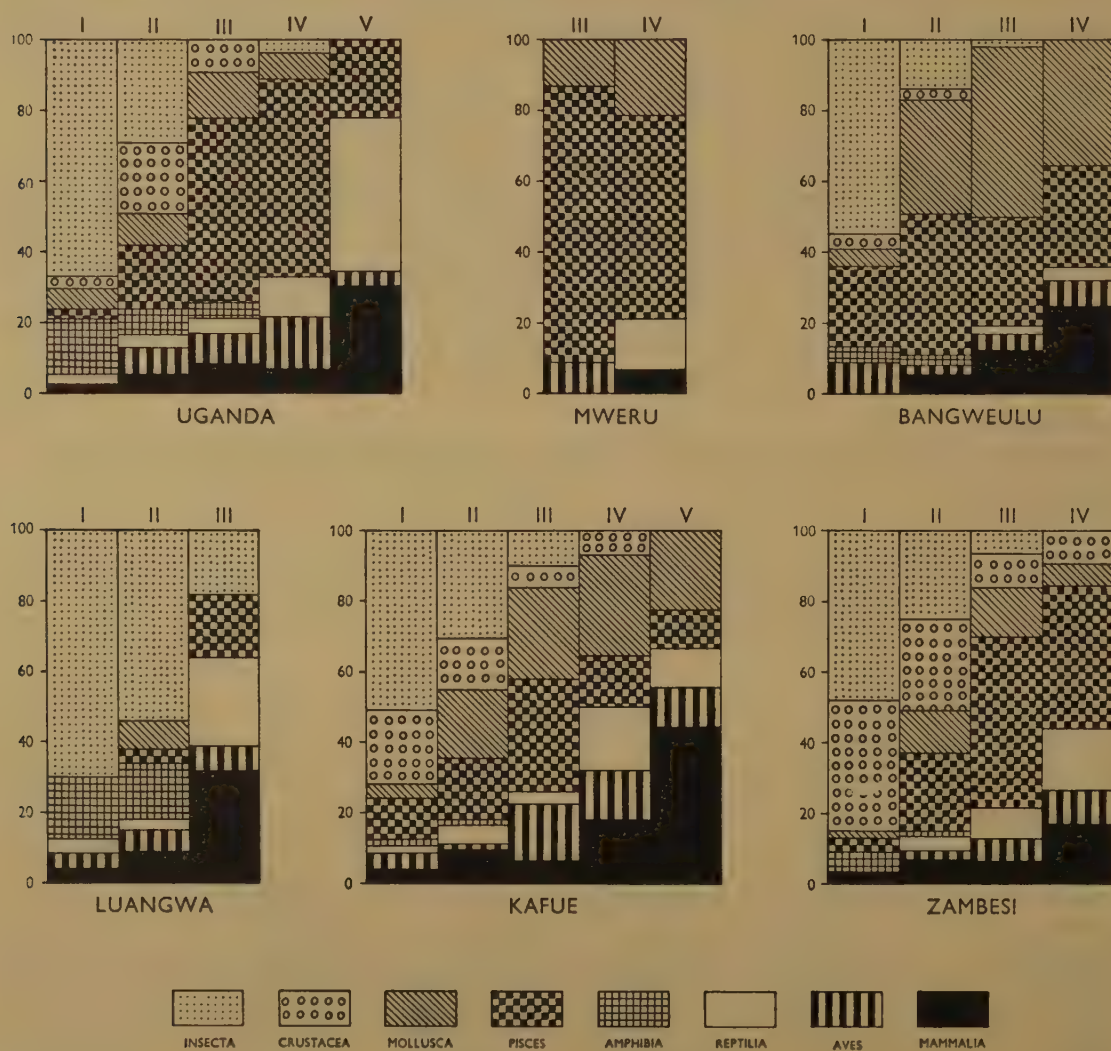


Fig. 37. Comparison of feeding habits of *C. niloticus* in six localities. The occurrences of each food category are expressed, for each Length Group, as a percentage of all occurrences.

TABLE 24

Number and percentage of stomachs containing various foods, by Length Groups: Mweru Wa Ntipa and Kalungwishi River.

<i>Length in metres</i>	<i>0-1</i>	<i>1-2</i>	<i>2-3</i>	<i>3-4</i>	<i>4-5</i>
Number of crocodiles containing prey	2	2	20	24	1
Insecta ..	2 (100·0%)	1 (50·0%)	—	—	—
Araneida ..	2 (100·0%)	—	—	—	—
Crustacea ..	—	—	—	—	—
Mollusca ..	2 (100·0%)	2 (100·0%)	3 (15·0%)	6 (25·0%)	—
Pisces ..	—	—	18 (90·0%)	16 (66·7%)	—
Amphibia ..	—	—	—	—	—
Reptilia ..	—	—	—	4 (16·7%)	—
Aves ..	—	—	2 (10·0%)	—	—
Mammalia ..	—	1 (50·0%)	—	2 (8·3%)	1 (100·0%)

TABLE 25

Number and percentage of stomachs containing various foods, by Length Groups: Luangwa Valley.

<i>Length in metres</i>	<i>0-1</i>	<i>1-2</i>	<i>2-3</i>	<i>3-4</i>
Number of crocodiles containing prey ..	17	49	20	1
Insecta	17 (100·0%)	41 (87·5%)	5 (25·0%)	—
Araneida	—	1 (2·0%)	—	—
Crustacea	—	—	—	—
Mollusca	—	6 (12·2%)	—	—
Pisces	—	3 (6·1%)	5 (25·0%)	—
Amphibia	4 (23·5%)	12 (24·5%)	—	—
Reptilia	1 (5·9%)	2 (4·1%)	7 (35·0%)	—
Aves	1 (5·9%)	5 (10·2%)	2 (10·0%)	—
Mammalia	1 (5·9%)	7 (14·3%)	9 (45·0%)	1 (100·0%)

TABLE 26

Number and percentage of stomachs containing various foods, by Length Groups : Kafue Flats.

<i>Length in metres</i>	<i>0-1</i>	<i>1-2</i>	<i>2-3</i>	<i>3-4</i>	<i>4-5</i>
Number of crocodiles containing prey	27	29	18	12	4
Insecta ..	25 (92.6%)	19 (65.5%)	3 (16.7%)	—	—
Araneida ..	3 (11.1%)	1 (3.4%)	—	—	—
Crustacea ..	10 (37.0%)	9 (31.0%)	2 (11.1%)	2 (16.7%)	—
Mollusca ..	2 (7.4%)	12 (41.4%)	8 (44.4%)	8 (66.7%)	2 (50.0%)
Pisces ..	5 (18.5%)	11 (37.9%)	10 (55.5%)	4 (33.3%)	1 (25.0%)
Amphibia ..	1 (3.7%)	1 (3.4%)	—	—	—
Reptilia ..	1 (3.7%)	3 (10.3%)	1 (5.5%)	5 (41.7%)	1 (25.0%)
Aves ..	2 (7.4%)	1 (3.4%)	5 (27.8%)	4 (33.3%)	1 (25.0%)
Mammalia ..	2 (7.4%)	6 (20.7%)	2 (11.1%)	5 (41.7%)	4 (100.0%)

TABLE 27

Number and percentage of stomachs containing various foods, by Length Groups : Zambesi.

<i>Length in metres</i>	<i>0-1</i>	<i>1-2</i>	<i>2-3</i>	<i>3-4</i>	<i>4-5</i>
Number of crocodiles containing prey	31	78	65	37	1
Insecta ..	25 (80.6%)	29 (37.2%)	6 (9.2%)	—	—
Araneida ..	7 (22.6%)	—	—	—	—
Crustacea ..	20 (64.5%)	31 (39.8%)	9 (13.8%)	5 (13.5%)	1 (100.0%)
Mollusca ..	1 (3.2%)	14 (17.9%)	13 (20.0%)	3 (8.1%)	—
Pisces ..	2 (6.5%)	26 (33.3%)	46 (70.8%)	21 (56.8%)	—
Amphibia ..	3 (9.7%)	1 (1.3%)	—	—	—
Reptilia ..	—	5 (6.4%)	8 (12.3%)	9 (24.3%)	—
Aves ..	—	3 (3.8%)	6 (9.2%)	5 (13.5%)	—
Mammalia ..	2 (6.5%)	8 (10.3%)	6 (9.2%)	9 (24.3%)	—

Uganda

The composition of insect food is remarkable for the high proportion of Hemiptera and Odonata : especially prominent are the giant water-bugs *Hydrocyrius columbiae* and *Limnogeton fieberi*, and the smaller *Sphaerodema nepoides*, as food of young crocodiles. The Uganda material shows a higher rate of predation on fish (Length Group III, 92·3 per cent.; Length Group IV, 79·0 per cent.) than has been found elsewhere, except in Mweru Wa Ntipa.

Bangweulu

A unique feature is the heavy intake of gastropods of the genus *Lanistes*. These large water snails were found in crocodiles of all length groups examined and—whether considered by bulk, by number of prey taken, or by occurrences—comprise the main food. The mean content per stomach containing food of any kind is 16·2 gastropods, as compared with 0·7 fish. Surprisingly, this local habit is shared even by the largest crocodiles. Thus : No. 127 (3·68 metres and the largest shot) contained no food other than 90 *Lanistes* ; No. H.64 (3·55 metres) contained 150 *Lanistes* ; and No. 124 (2·55 metres) had its stomach distended with 820 *Lanistes* and remains of two fish. Notable deficiencies from the diet of these swamp crocodiles are crabs (2 only), anura (3 only) and turtles (none).

Mweru Wa Ntipa

Nothing is known of the feeding habits of the young. Those of the adults are specialised, and indeed crocodiles living in the highly opaque, alkaline waters of this shallow lake appear to be almost monophagous. Thirty-seven of fifty-one crocodiles over 2·5 metres contained food, and of these thirty had been feeding on *Clarias mossambicus*. No *Tilapia* were recovered. Occurrences of other prey were limited to molluscs (4), crocodile remains (3), birds (1) and mammals (2).

Luangwa Valley

The food of crocodiles in the Lunsemfwa and Luangwa Rivers again shows certain distinctive features. Beetles are preyed upon more extensively than elsewhere and the insectivorous habit persists longer in life. Prominent are various terrestrial insects, notably *Gryllotalpa africana*, *Cicindela dongalensis*, *Scarites aestuans* and *Temnorhynchus* spp.; while surprisingly few water beetles (Dytiscidae, Hydrophilidae) were found. Other notable deficiencies in the diet are crabs (none), molluscs (6 occurrences) and fish (only 8 occurrences in 87 stomachs containing food). Anura and reptiles occur frequently, and in greater variety than elsewhere ; and rodents, especially cane rats, are the main mammalian prey.

Kafue and Zambesi Rivers

Beetles are the most frequent food of the young, *Hydrophilus aculeatus* being

an important prey species. In certain other respects the diet differs markedly from that in the Luangwa Valley. Fresh water crabs, *Potamonautes*, were taken by crocodiles of all sizes, including the largest, and appear to form the bulk of all food of juveniles up to about 1.2 metres in the Kafue and up to about 1.5 metres in the Zambesi. Anura were rarely taken (only six occurrences in 303 stomachs containing food). Both molluscs and fish become important prey in adult life, the former especially in the Kafue and the latter in the Zambesi.

Feeding behaviour

The Nile Crocodile is remarkable for the wide variety of prey taken in the course of its life. Victims range from terrestrial and aerial to wholly aquatic forms ; and in size from small organisms such as spiders, ants and termites, up to the great mammals and including African Buffalo (Andersson, 1856 ; Pitman, 1936, 1949), Lion, Black Rhinoceros (Selous, 1908 ; N.R. Journal, 1950), and Camel (Owen, 1951).

Its methods of hunting, capture and disposal of prey are as varied as the habits of its victims. Thus no general statement regarding feeding techniques is admissible, though it may be said that nearly always stealth, surprise, and a sudden final burst of speed are involved.

Methods of attack

The method of attack depends upon circumstances : the approach may be (a) from water to land ; (b) from water to air ; (c) on land ; and (d) under water.

(a) Adult crocodiles often lurk off-shore near game trails and watering places. On sighting an animal that has come down to drink, the reptile quietly submerges, and cruises under water to the precise spot from which it can make its fatal upward rush. The prey is seized by the nose or leg, dragged back into the water, and drowned.

(b) The under-water approach is also used when crocodiles are feeding upon flocks of weavers at their overhanging nests (Baker, 1871), or in attacks upon *Quelea* during their evening drinking ritual (Attwell, 1954). The speed of the final assault is instantaneous. At Jinja I have seen a swimming crocodile take a dragonfly on the wing, the jaws closing over the insect like a sprung gin. On the Zambesi a crocodile has been seen to catch a leaping tigerfish (*Hydrocyon*) in mid-air (Voigt, 6.10.56).

(c) The habits of young crocodiles when feeding on land are similar to those of an insectivorous lizard : either the animal snaps at insects that pass or alight within reach—sometimes jumping into the air to do so ; or else it scrambles in search of beetles and other more sluggish prey.

When feeding ashore, adults often lie in ambush near trails or beside dried-up water courses that are used by waterbuck and other game coming to drink. It is under such circumstances that the deadly tail-stroke or sledge-hammer head-blow take effect—to throw the victim, break its leg, or fling it into the water.

(d) Two main methods of fishing—passive and active—have been observed. When feeding on small fish in-shore, crocodiles will lie submerged and motionless, with the mouth open and awash, and snap up prey as the shoals swim within reach (Stevenson-Hamilton, 1954 ; Holloway, pers. comm.).

Crocodiles have often been observed fishing in open water (Carpenter, 1928 ; Hubbard, 1927 ; Pitman, 1929 ; Graham, 1929 ; Salmon, 1932, and others) ; and further evidence that they take actively swimming fish is afforded by their seizing the plug-baits of anglers (Kinloch, 1956). The various accounts agree as to the procedure : the crocodile disappears under the water, hurls itself at its prey with a sudden plunge. It then surfaces, thrusting its head out of the water and smacks its jaws to kill and manipulate the fish until it can be swallowed head first.

Disposal of prey

The popular belief that crocodiles store bulky prey in “larders,” and that they prefer their meat when it is partly decomposed, does not appear to be generally true. And despite what has often been said to the contrary, crocodiles are well able to feed from a large, fresh carcass.

According to Major W. E. Poles (1951), who watched crocodiles feeding on a hippopotamus in the Luangwa, the initial penetration is effected with an upward and sideways slash delivered with the lower jaw, the fourth tooth of which is admirably adapted for a spear thrust. Once the jaws are locked, the crocodile executes a slow roll, and so tears off a portion. Sometimes the reptile will roll right round half a dozen times in succession to detach a piece of meat. Smaller mammals are speedily dismembered in this fashion.

Food is always brought to the surface to be swallowed. Sometimes, as reported by Percival (1928) a large siluroid may be taken ashore and battered to death on a rock. Anderson (1950) saw crocodiles take catfish from pools of the Ibba onto a sand bank, where they ripped the flesh of the back and tail from the still living prey.

Scavenging

As scavengers, crocodiles fill the same niche as that occupied by vultures, marabou and hyaenas in the economy of nature. They readily assemble, especially at night, to feed on a carcass, and have frequently been observed in the water dismembering buffaloes, zebra, waterbuck or the carcasses of crocodiles discarded by skinners. Savidge (*in litt.*, 27.4.57) saw a crocodile feeding at the carcass of a lion that had been killed by buffaloes above Murchison Falls.

If the carcass is on shore, the reptiles often drag it into the water, where they can more readily, and in greater safety, dispose of it. Pitman (1939) reports that crocodiles he had shot were sometimes dragged to the lake through 30 or 40 yards of forest. But often these scavengers will come inland to feed from a kill (Attwell, 1959) ; and in the Semliki Valley Mr A. M. Henley once found four crocodiles feeding at the carcass of an elephant that had died half a mile from the river.

ENEMIES

Being the master predator in its environment, the adult crocodile has little to fear from any aggressor—except man. But various enemies take a heavy toll of both eggs and young.

Egg predators

The most important enemy is undoubtedly the Nile Monitor (*Varanus niloticus*) (Plate 7, fig. 2). In Uganda, wherever crocodiles are found in the breeding season, there the monitors are in active attendance. And on almost every nesting ground their scrapes and the surrounding litter of discarded egg-shells tell the tale of destruction. Mitchell (5.6.57) records that in Northern Rhodesia monitors appear to take the majority of clutches laid; and Player (3.2.60) also reports heavy predation by *V. niloticus* in Zululand.

When foraging for eggs, the lizards show little fear of the crocodile, often walking close alongside to make exploratory scrapes within a few feet of its flanks (Plate 8, fig. 1). Sometimes they employ a ruse to entice a guardian crocodile from her eggs. Pitman (1931) on more than one occasion saw a monitor provoke a female to chase it into the water, while its mate speedily excavated the nest, later to be joined by the individual that had lured the crocodile away. Hippel (25.4.52) tells me he has also seen monitors working thus in pairs—which he believed to be the male and female—near Bugonda, Lake Kioga. However, their best chance of booty comes when the crocodiles have been disturbed. At such times half-a-dozen or more of the lizards will appear from nearby cover, to conduct on the deserted grounds a persistent search for eggs.

Defence of the eggs by the crocodile is mainly passive—each female lying over her clutch. But Mr Douglas Jones told me he once saw crocodiles go into action against the marauders. As his launch drew near one of the beaches at Fajao, the crocodiles walked into the water: however, while the monitors were taking advantage of their absence, several returned and sent the lizards scurrying from the site. Such counter-attacks have rarely been witnessed: but the presence of monitors in crocodiles' stomachs—from Murchison, Uganda (No. 36), the Luangwa, Kafue and Zambesi Rivers, Northern Rhodesia (Nos. 254, 259, 265, 374, V. 21), Upper Zambesi, Barotseland (Nos. 481, 510), and the Usutu River, Zululand (No. Pl. 1)—indicate that the egg thieves are often caught unawares.

The Marabou (*Leptoptilos crumeniferus*) is known to eat the eggs. In 1955, at two places below Murchison Falls, Douglas Jones watched these carrion-feeders gorge themselves on clutches that had been uncovered by monitors. Goldsmith (1805) states that vultures watch the crocodile laying, and later tear up the eggs: Ellis (1838) also refers to egg-eating by vultures in Madagascar.

Mammalian egg thieves include mongooses, baboons and hyaenas. Many early writers refer to the mongoose's hostility to the crocodile. In Egypt the culprit would presumably be *Herpestes ichneumon* (Anderson 1898). According to Stevenson-Hamilton (1954) the Water Mongoose (*Atilax paludinosus*) is one of the most deadly enemies in southern Africa. Mitchell (1946) records that many

nests are dug out by the Spotted Hyaena (*Hyaena crocuta*) in Nyasaland ; and in Uganda this habit has been confirmed by Pitman (27.5.59).

Olive Baboons (*Papio anubis*) often visit the crocodile beaches when on their way to water, and have opportunity to steal unguarded eggs. Mr John Savidge (12.2.57) tells me that at three separate places in one day he has seen baboons sitting close beside crocodiles : as soon as the reptiles had been frightened into the water, the baboons scrambled to the place where they had been lying to dig up and eat the eggs.

According to Lavauden (1934) eggs are also taken by Warthogs and Bush-pigs.

Enemies of the young

The newly-hatched young are relatively defenceless, and they doubtless fall victims to a variety of enemies both on land and when first launched upon life in the shallows.

From the evidence of stomach contents, and from observations on captive specimens, it would appear that older crocodiles are an agent of infantile mortality. Again, monitors certainly do not confine their attentions to the eggs. Anderson (1898) states that when the young make from the nest to the water, they fall a prey to *V. niloticus*. Charles Magala assured me that he had himself seen the lizards preying upon recently-hatched young ; and Mr R. M. Bere (17.5.56) refers to the heavy toll taken by both monitors and marabou, below Murchison Falls, when the eggs are hatching.

According to various early accounts from Egypt (Sonnini, 1800 ; Borderip, 1852 ; Burton, in Anderson, 1898) a turtle called Thirse—which is presumably *Trionyx triunguis* (Flower, 1933)—also takes heavy toll when the newly-hatched young repair to the river. Both at the Magungu and Fajao crocodile grounds these large turtles were often seen, and they were found breeding at the former site. From the Congo, Hoier (1950) reports predations by catfish.

Mr I. H. Player tells me that both he and Mr L. Trollope have seen baby crocodiles taken by the Fish Eagle (*Cuncuma vocifer*) in Zululand. Livingstone (1865) had previously recorded that fish-hawks make havoc among the young. Marabou also take their toll at hatching time (Bere, 17.5.56). Finally, Mr John Savidge (27.4.57) sends me circumstantial evidence from Murchison that the Ground Hornbill (*Bucorvus abyssinicus*) must be numbered among their enemies.

Enemies of the adult

The animal with which adult crocodiles are most likely to come into conflict is the hippopotamus. The species often meet and intermingle, both on land and in the water, and their relations are those of armed neutrality. On land, the hippopotamus is the acknowledged master and the reptiles readily give ground before them, sometimes hissing remonstrance as they retreat. At Fajao in 1952 Major Roy Wyndham saw two males—which were about to fight—first clear the arena by pushing all the crocodiles from their basking place. Stevenson-Hamilton

(1954) states that at calving time either the mother or others of the school will drive all the crocodiles out of the pool in which they happen to be lying. When protecting her calf in the water, a female will snap viciously at any crocodile that ventures too close. Sometimes the attack is pressed home and the crocodile is seized and bitten in half. Evidence of such an assault is reported from the Pafuri River by Stevenson-Hamilton (1954) ; and on 26th July, 1956, near Paraa, I saw a crocodile lying in the shallows in two pieces—its body completely severed just in front of the hind limbs. Further evidence of such encounters is given by Poles (1953) and by Mr J. E. Tully (personal communication).

The only other animals that are known to kill adult crocodiles are the Lion, Leopard and African Elephant. Crocodiles are quick to take advantage of another animal's kill, and Stevenson-Hamilton (1954) heard one reliable instance of a crocodile being killed by lions in such an encounter. A remarkable incident is recorded by Cameron (1877) in which a crocodile interfered in a lion and buffalo fight—all three animals eventually perishing.

It is an indisputable fact that lions sometimes deliberately prey upon the reptiles. Salmon (1932) described such an occurrence—the first recorded from Uganda—at Butiaba, where in August 1931 a lion, having killed a large crocodile measuring 11 feet, 7 inches, consumed the neck, shoulder and flanks. Pitman (1942) also reports that one afternoon visitors to the Murchison Falls saw a lion stalk and kill a crocodile on the opposite bank : the creature was so hungry that it continued to feed even when the launch crossed the river to afford a closer view. According to Thomas & Scott (1949) lions have been known to kill and devour crocodiles on the Lake Albert flats. Salmon (*ibid.*) also states that crocodile killing by lions "has been recorded as quite a normal occurrence on the western shore of Lake Rudolf."

Mr R. I. G. Attwell tells me that in the Luangwa Game Reserve, in June 1957, a crocodile moving from one drying pan to another was killed by a leopard, which later returned and ate half the tail.

According to Maberly (1959) there are several records of elephants having attacked and killed crocodiles—especially when the reptiles had been encountered travelling overland. In the Rufiji, elephants are reported to have placed their crocodile victims up in trees (Barker, 1953).

INJURIES

Injuries of various kinds—wounds, scars, fractures and amputations—were frequently observed in the specimens examined (Plate 6, figs. 1 to 4). Data under this heading are recorded for 548 crocodiles : of these, 113 (about 20 per cent.) had sustained 127 injuries varying in severity from minor damage to serious mutilations. As might be expected, injuries are more frequent in older than in younger animals. This cumulative effect is shown in the following tabulation :

<i>Length Group</i>	<i>I</i>	<i>II</i>	<i>III</i>	<i>IV</i>	<i>V</i>
Number examined	119	178	156	84	11
Number injured . .	8	25	36	37	7
Per cent. injured	6.7	14.0	23.1	44.0	63.6

In the collections from each of the seven localities listed in Table 28, the tail is the part most often damaged. For the whole series, injuries are distributed as follows : tail, 89 (70.1 per cent.) ; limbs, 18 (14.2 per cent.) ; head, 14 (11.0 per cent.) ; body, 6 (4.7 per cent.).

Direct evidence as to the agents responsible for the damage is generally wanting. Several crocodiles from the Upper Zambesi (Nos. 419, 420, 439, 454 and 468) had one or more of the barbed pectoral or dorsal fin spines of *Synodontis* firmly fixed in the palate or tongue. In other cases, it is probable that most of the injuries were inflicted by crocodiles, either in inter-male combat (see p. 267) or in the course of attacks by potential cannibals (see p. 296). The latter may account for many of the caudal lesions. If, on the other hand, injuries are received in combat between males, this would be reflected in their higher incidence among mature males than among mature females. Comparative data for the sexes (see Table 28) support the view that much of the damage is sustained in this way. The upper graphs in Fig. 38 show, for the sexes separately, the percentage with injuries. (In the absence of knowledge concerning the growth rate in adults, the comparison has here to be made in terms of length rather than age. When

TABLE 28

Incidence of injuries, in relation to sex and crocodile length.

Locality	Crocodile length in metres									
	0.3-1.0		1.0-2.0		2.0-3.0		3.0-4.0		4.0-5.0	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Uganda	2	1	2	2	2	1	3	4	4	—
Bangweulu	—	—	0	1	2	1	2	1	—	—
Mweru Wa Ntipa	—	—	—	—	2	1	5	1	0	—
Kalungwishi R.	—	—	0	1	0	1	2	0	—	—
Laungwa Valley	0	1	3	2	3	1	0	1	—	—
Kafue Flats	1	2	3	1	3	2	3	5	3	—
Upper Zambesi	1	0	5	5	8	9	6	4	—	—
No. examined	55	46	85	92	71	85	45	39	11	—
No. injured	4	4	13	12	20	16	21	16	7	—
Per cent.	7.3	8.7	15.3	13.0	28.2	18.8	46.7	41.0	63.6	—
No. seriously injured	2	1	4	1	5	0	6	3	4	—
Per cent.	3.6	2.2	4.7	1.1	7.0	0.0	13.3	7.7	36.4	—

allowance is made for the fact that females attain maximum growth over a size range that is at least one metre below that of fully-grown males, the divergence in the proportions of injured adult males and females will be greater than appears from the data as here presented.) The discrepancy becomes far more striking if account is taken only of severe casualties (see Table 29 and lower graphs, Fig. 38) : among twenty-six crocodiles showing evidence of more or less disabling mutilations, no fewer than twenty-one (about 81 per cent.) were males.

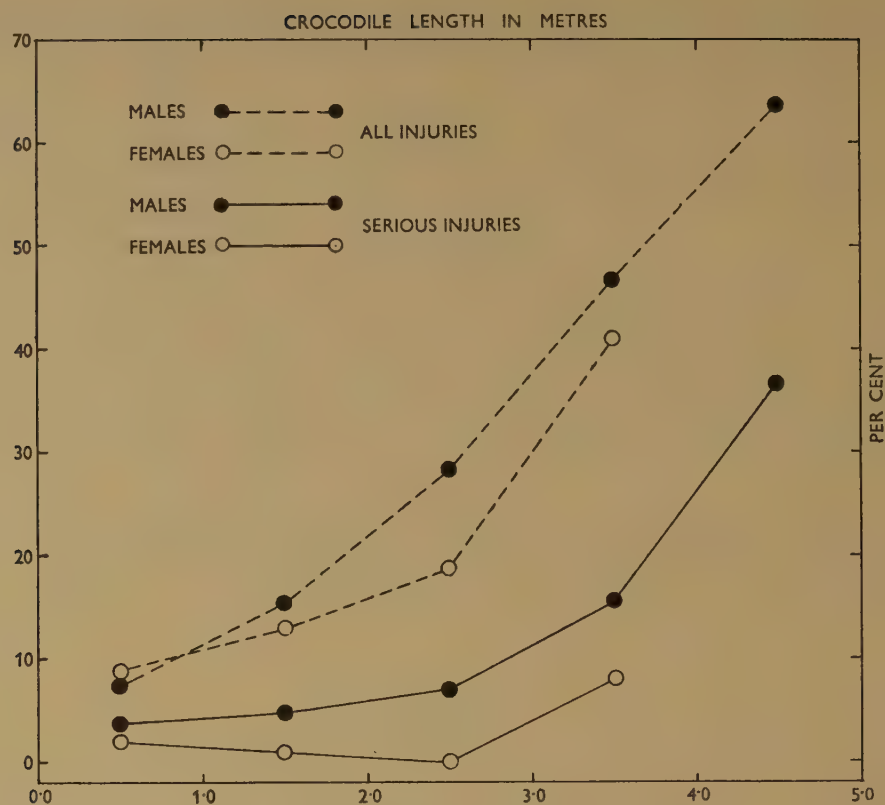


Fig. 38. Injuries, in relation to sex and length.

TABLE 29

List of serious (more or less disabling) injuries.

<i>Serial No.</i>	<i>Locality and Date</i>	<i>Length in mm.</i>	<i>Sex</i>	<i>Nature of injury</i>
1	Jinja, L. Victoria ; 9.1.52	c.1110	♂	distal half of tail missing ; wound healed with regenerated cornification.
17	Ntoroko, L. Albert ; 17.6.52	2750	♂	wound in groin.
27	Ripon Falls, Nile ; 8.7.52	3117	♀	right fore limb amputated at shoulder ; injury healed with pad of regenerated scales. (Plate 6, 2).
44	Buluba, L. Victoria ; 22.8.52	c.690	♀	distal half of tail missing behind penultimate paired caudal scutes.
124	Bangweulu Swamp ; 23.8.56	2550	♂	distal rami of lower jaw amputated at level of 5th tooth in upper jaw ; injury healed ; anterior teeth of upper jaw recurved. (Plate 6, 3).
178	Mweru Wa Ntipa ; 14.9.56.	c.3820	♂	tail amputated behind 7th median scute.

(continued next page)

Table 29—*continuation*

<i>Serial No.</i>	<i>Locality and Date</i>	<i>Length in mm.</i>	<i>Sex</i>	<i>Nature of injury</i>
180	Mweru Wa Ntipa ; 14.9.56	3520	♂	deep gash at base of left rear limb.
190	Mweru Wa Ntipa ; 14.9.56	2860	♂	distal rami of lower jaw amputated at level of 4th tooth in upper jaw ; dental abnormalities (Plate 6, 4).
193	Mweru Wa Ntipa ; 15.9.56	3380	♂	abnormal growth of snout resulting from serious injury in the nasal region (Plate 6, 1).
223	Magungu, Victoria Nile ; 2.1.57	4220	♂	a long open festering wound, infested with leeches, at base of tail, dorsally ; several median dorsal tail scutes missing ; tail tip amputated.
S.1	Magungu, Victoria Nile ; 23.4.57	c.4460	♂	four scars of old wounds, from 9 to 17 cms. long, on tail ; 4 scars on belly ; end of tail missing ; 4th digit of left fore limb fractured.
229	Rufunsa, Lunsemfwa R. ; 2.8.57	c.1030	♂	tail amputated behind 9th median scute.
273	Rufunsa, Lunsemfwa R. ;	c.2800	♂	tail amputated behind 8th median scute ; caudal scutes missing ; wound scars dorsally above hind limbs, and at base of tail.
299	Beit Bridge, Luangwa R. ; 11.8.57	950	?	rami of lower jaw amputated at level of 6th tooth in upper jaw ; regenerated with new symphysis.
305	Ndevu, Luangwa R. ; 13.8.57	c.1500	♀	tail amputated behind 3rd median scute.
337	Chimwajila, Kafue R. ; 24.8.57	4350	♂	tail tip missing ; upper jaw injured with many anterior teeth missing ; 10 cm. gashes on side of tail and behind right shoulder ; deep wound on right side of neck.
343	Chimwajila, Kafue R. ; 25.8.57	4270	♂	long gash dorsally at base of tail ; left fore limb fractured and deformed.
386	Iyeshya, Kafue R. ; 30.8.57	3540	♂	scars of two severe gashes, beneath throat and behind vent.
398	Iyeshya, Kafue R. ; 31.8.57	c.1370	♂	tail fractured at mid-length ; amputated behind 13th median scute ; 5 median dorsal scutes missing.
410	Iyeshya, Kafue R. ; 1.9.57	775	♂	severe regenerated injury at base of tail behind vent.
416	Mongu, Upper Zambesi ; 10.9.57	c.3040	♂	end of tail amputated ; severe gashes ventrally in mid sector of tail.
428	Mongu, Upper Zambesi ; 10.9.57	885	♂	scars of severe bites ventrally at base of left hind limb.
450	Mongu, Upper Zambesi ; 13.9.57	3120	♀	lower jaw broken at symphysis ; injury regenerated but jaws closing asymmetrically.
481	Mongu, Upper Zambesi ; 15.9.57	c.3490	♂	tail amputated behind 10th median scute.
483	Mongu, Upper Zambesi ; 15.9.57	2910	♂	severe caudal injury, with large festering sore.
519	Mongu, Upper Zambesi ; 16.9.57	1890	♂	segment of muzzle missing, right side.
532	Mongu, Upper Zambesi ; 18.9.57	3130	♀	wedge-shaped portion of muzzle missing anteriorly, right side.

PARASITES

Tsetse flies

In Uganda the tsetse fly *Glossina palpalis* is a common parasite of the crocodile. Both in Lake Victoria and along the Murchison reach of the Nile the flies were frequently observed settled, and feeding, on the thin skin between the scutes and on the tongue and mucosa (see Plate 2, fig. 2).

At Entebbe, Hoare (1929) experimentally carried the crocodile trypanosome, *T. grayi*, through its entire life-cycle, from naturally infected flies to the crocodile and from the crocodile to the flies again. Hoare (1931) also found that the degree of infection among "wild" tsetse flies compared closely with that among experimental flies that had fed only on crocodiles; hence he inferred that in Lake Victoria the blood of the crocodile is the main food of the fly.

That the tsetse prefers reptilian to mammalian blood is also indicated by the fact that where crocodiles are abundant, as at Magungu, *G. palpalis*, though plentiful, is hardly troublesome to man. On the other hand, Marlier (1954) has stated that in areas of the Ruzizi basin where crocodiles were scarce, tsetse flies were less numerous but attacked man more vigorously.

The intimacy of the association between *G. palpalis* and *C. niloticus* is further shown by the fact that this fly is also the intermediate host of another crocodile blood parasite—the haemogregarine *Hepatozoon pettiti* (Hoare, 1932).

Leeches

Crocodiles are commonly infested, in some degree, with leeches. From samples, collected, the following have been identified: *Placobdella fimbriata*, from Jinja, Buluba (L. Victoria), Ripon Falls (Victoria Nile), and Kigi Is. (L. Kioga); ? *Helobdella conifera*, from Jinja; and *Placobdella jaegerskioeldi*, from Mweru Wa Ntipa, and L. Chali (Bangweulu).

Leeches were present on 174 out of 506 crocodiles for which data are available. Table 30 summarises the information collected.

TABLE 30
Occurrence of leeches, in relation to crocodile length, for different localities.

Locality	Crocodile length-groups									
	I		II		III		IV		V	
	No. examined	No. with leeches	No. examined	No. with leeches	No. examined	No. with leeches	No. examined	No. with leeches	No. examined	No. with leeches
Uganda	39	5	17	4	10	6	12	10	6	6
Bangweulu Swamp ..	10	0	9	3	17	13	7	5	—	—
Mweru and Kalungwishi R.	2	0	2	1	24	6	32	18	2	1
Luangwa Valley ..	14	0	51	7	20	0	1	1	—	—
Kafue Flats	31	0	30	2	15	7	11	5	3	3
Upper Zambesi	11	0	53	21	59	40	18	10	—	—

The main point that emerges from this study is that infestation tends to increase progressively throughout the crocodile's life: this is true both as regards occurrence (see Fig. 39) and degree of infestation (see below). In their first year, the young are entirely free: the percentage occurrence rises from 4.7 per cent. in Length Group I, to 90.9 per cent. in Length Group V. This trend was generally similar for all the localities studied, except the Luangwa Valley (see Fig. 40).

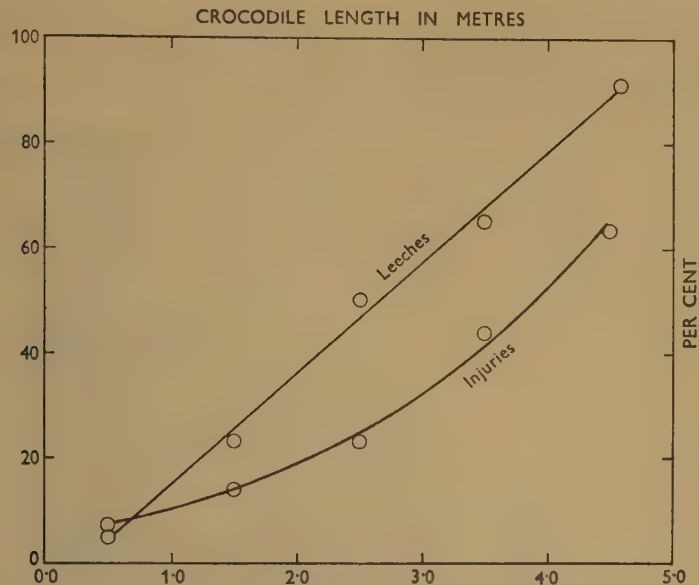


Fig. 39. Changes in the percentage of crocodiles carrying leeches, and with injuries, in relation to growth.

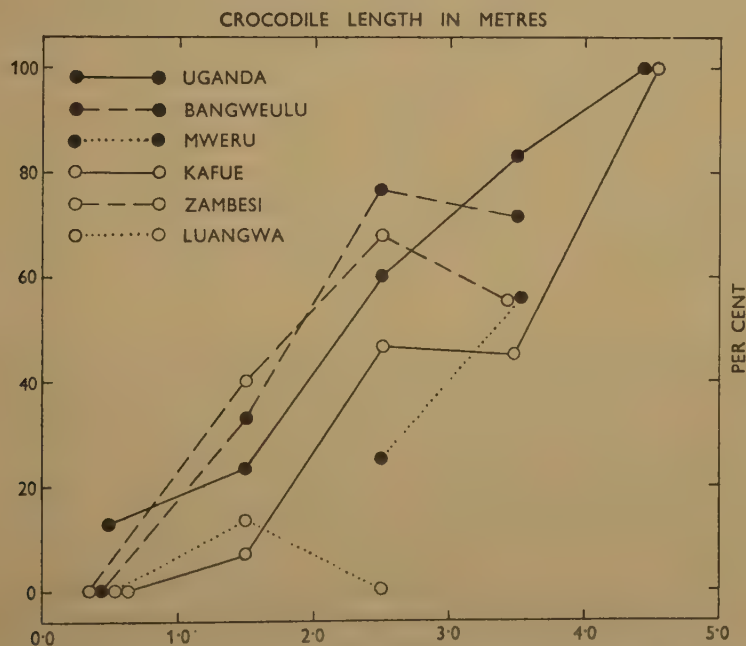


Fig. 40. Leech infestation: showing percentage of crocodiles carrying leeches in different localities, and in relation to crocodile length.

The incidence rate was exceptionally low (9.3 per cent.) in the Luangwa ; and highest in Bangweulu (48.8 per cent.) and the Upper Zambesi (50.4 per cent.).

Three degrees of infestation are here recognized : light—from one, to a cluster of about ten leeches ; moderate—two or more clusters ; and heavy infestation—for example, No. 112 carried about 150 leeches. Occurrences, in different degrees of infestation, are summarised below, and shown graphically in Fig. 41.

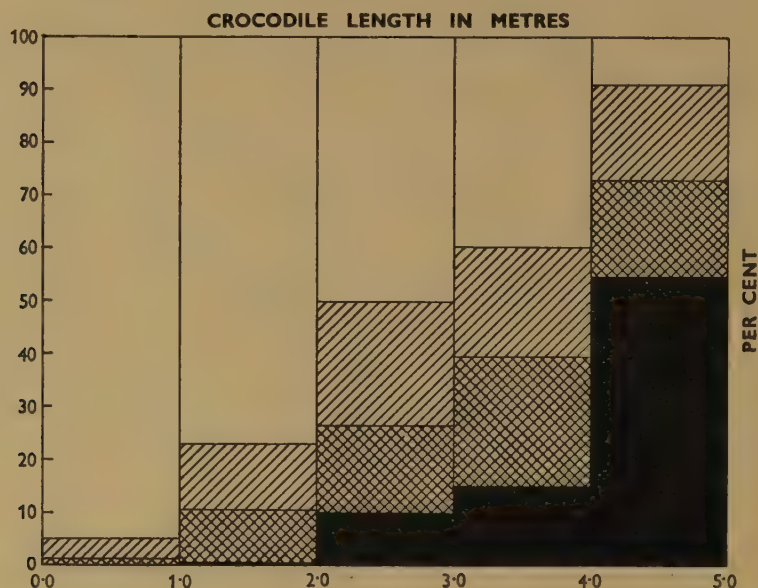


Fig. 41. Histogram showing percentages of different degrees of leech infestation in relation to crocodile length. Black—heavy ; cross-hatched—moderate ; diagonals—light ; white—nil.

Length Group			I	II	III	IV	V
Number examined	107	162	145	81	11
Light infestation	4	21	34	17	2
Moderate infestation	1	16	24	20	2
Heavy infestation	0	1	14	12	6

Leeches may be found attached to any part of the body. Large concentrations were often present on the site of old scars, festering sores, and in dental sockets (Plate 6, fig. 4). Occurrences (in any degree of infestation) were distributed as follows : muzzle, head and nuchals, 3 ; shoulder, dorsal scutes and flanks, 32 ; fore limb, 24 ; armpit, 27 ; hind limb, 87 ; groin, 37 ; tail, 12 ; cloaca, 29 ; ventral shields, 28 ; gular shields, 14 ; tongue, teeth and mucosa, 23. In relation to the surface available for attachment, inaccessible parts, such as the cloaca, groins and armpits were far more heavily infested than the large exposed surfaces of the head, back, flanks and tail. It is not improbable that the leech-gathering activities of commensal birds (see p. 315) may account, in part, for the very uneven distribution observed.

Nematodes

Conditions under which the field work was carried out did not permit of a routine study of internal parasites ; and information under this head is meagre. The commonest obvious parasites were nematodes. These were found in forty-four of sixty-six stomachs examined in Uganda, and in this sample were distributed in length-groups as follows :

<i>Length Group</i>	<i>I</i>	<i>II</i>	<i>III</i>	<i>IV</i>	<i>V</i>
Number examined	33	17	7	7	2
Number with nematodes ..	25	10	3	4	2
Occurrence per cent. ..	76	59	43	57	100

Two species are represented : *Multicaecum agile*, from Jinja and Namasagale ; and *Dujardinascaris dujardini*, from Jinja, Buluba, Damba and Kaiso.

Nematodes recovered from stomachs in other localities include *D. dujardini*, from Iyeshya (Kafue R.) ; and *Contracaecum* sp., from Chimwajila (Kafue R.). Mr W. G. Inglis, who examined the material, tells me that the specimens of *Contracaecum* were almost certainly derived from fish : both the other nematodes are specific to the crocodile.

COMMENSAL BIRDS

Birds of many kinds—including darters, herons, egrets, duck, plovers, waders, skimmers and wagtails—frequent the basking and breeding grounds ; and in such places become casually associated with the crocodile. Thus, at Magungu, Goliath Heron (*Ardea goliath*), Little Egret (*Egretta garzetta*) and Egyptian Goose (*Alopochen aegyptiacus*) were often found close to the reptiles. Below Murchison Falls, White-Collared Pratincole (*Galachrysis nuchalis*) and Pied Wagtail (*Motacilla aguimp*) frequented the rock islets when these were covered with crocodiles. At Ntoroko, on the Semliki, I have seen crocodiles closely attended by Hadada (*Hagedashia hagedash*) and Sacred Ibis (*Threskiornis aethiopicus*), Goliath and Great White Heron (*Casmerodius albus*), besides the more regular companion birds—Spur-Winged Plover (*Hoplopterus spinosus*) and Water Dikkop (*Burhinus vermiculatus*). On the Paraa-Fajao reach of the Nile, certain shelving mudbanks were often covered with White-faced Duck (*Dendrocygna viduata*) resting among lines of crocodiles : some of these banks were also the resort of African Skimmers (*Rynchops flavirostris*).

In such cases the association is fortuitous, the birds and reptiles merely sharing a common resting place. When lying ashore the crocodiles seem never to interfere with their companions ; and the birds approach these potentially dangerous predators on the most familiar terms. For example, Chapman (1921) observed a large flock of Crowned Cranes (*Balearica pavonina*) placidly sleeping among crocodiles. On a mudbank in Lake Albert, Eggeling saw a crocodile surrounded by Knob-bill Geese (*Sarkidiornis melonotos*)—four of which were actually perched on its back (Pitman 1935). And Player (19.7.55) tells me that in Zululand he has observed White-faced Duck walking all over the bodies of crocodiles. This tolerance shown by basking crocodiles (which in other circumstances habitually prey

upon waterfowl) throws indirect light upon the special associations next to be considered.

The classical account of a bird which was supposed to attend the crocodile in Egypt, as given by the early natural historians, is well known. In Pliny's version of the narrative, the crocodile-bird was said to take scraps of food that remained sticking to the reptile's teeth. Herodotus is more explicit: ". . . the crocodile . . . is in the habit of lying with its mouth wide open, facing the western breeze: at such times the *Trochilos* goes into his mouth and devours the leeches. This benefits the crocodile, who is pleased, and takes care not to hurt the *Trochilos*" (Rawlinson's trans.).

The identity of the *Trochilos* was much debated in the last century. St. Hilaire (1827), Taylor (1859, 1867), von Heuglin (1869), Dresser (1871-81), and Newton (1893-96) were among those who sustained the claim for the Egyptian Plover (*Pluvianus aegyptius*). Others, including Broderip (1852), Adams (1864), Smith (1868), Cook (1892) and Butler (1905) adduce evidence that the crocodile's benefactor is the "Zic-zac" (*H. spinosus*). Those who have disputed the rival claims of these birds all assume that the classical authors referred to one particular species. In the light of what is now known from other parts of Africa (see below) it is probable that *P. aegyptius* and *H. spinosus* were both associated with the crocodile in Egyptian waters.

For a long time the story was put down as one of the old Greek myths; and despite observations of St. Hilaire, Brehm, Cook and Burton—all of whom claimed to have seen plovers take food from the crocodile's mouth, some authorities, including Anderson (1898), Flower (1908), Bannerman (1930-51), and Cave & Macdonald (1955) have remained sceptical. For example, Bannerman states: "The popular belief . . . does not find much favour amongst competent naturalists at the present day."

Turning to present observations: in Uganda, *H. spinosus* is the crocodile's constant companion on all the favoured basking grounds on the shores and islands of Lake Victoria, along the Victoria Nile, and in Lake Albert and the Semliki River. The birds live on terms of intimacy with their partners and may constantly be seen running from one reptile to another, flitting over the sprawled bodies, and foraging or standing beside them (Plate 9, figs. 1 and 2). I have seen a pair standing within a foot of the gaping jaws. At Magungu, and elsewhere, the plovers are probably attracted by tsetse flies (*G. palpalis*) which depend mainly upon the crocodile for their blood supply. There is no reason to doubt that the agile and ever-alert *Hoplopterus* can, with impunity, snap at flies and leeches from the mucosa. Mr J. D. Kelsall assured me that in southern Lake Victoria he once observed a "crocodile-bird" (unidentified) jump from the ground to take something from the upper jaw of a gaping crocodile; and Hobley (1919) states that on the Nzoia River near Mumias he saw a Grey Wagtail walking about inside the open mouth. In this connexion, it is relevant to note the closely-parallel and well-authenticated association in small tropical fish (*Elacatinus oceanops*) which enter and clean the mouth cavity of the grouper *Epinephelus* (Eibl-Eibesfeldt, 1955).

Another bird that habitually feeds from basking crocodiles is the Common

Sandpiper (*Actitis hypoleucos*). During long periods in the hide at Magungu I frequently observed this habit. To cite one example, the following is taken from my journal, 30.12.56: "At 0945 hrs. a large crocodile waded boldly out of the river and planted itself squarely on the foreshore. . . . Almost immediately it had settled, a common sandpiper ran up to it and ran along beside its tail, starting from the hind limb and working towards the tail-tip, snapping at insects (probably tsetse flies) as it went (see Plate 9, fig. 3). Once it jumped from the ground to catch an insect otherwise out of reach. . . . This sandpiper returned on at least four occasions to work round the crocodile." The birds usually paid particular attention to crocodiles which had just come ashore: on one morning a sandpiper hurried up to four or five crocodiles in turn, while each was still wet from emergence.

In Zululand I. H. Player and K. Tinley have independently made similar observations, which both confirm and extend my own. On different occasions at Lake Nyamiti, Ndumu Game Reserve, sandpipers were seen—to peck at something in a crocodile's mouth; to stand on the upper jaw; to remove a leech from the gular scutes; and to stand on the lower jaw and take a leech from the mucosa (Player, 24.3.55). Player and Tinley have also seen a Common Sandpiper run up to a turtle that had just come ashore and pick leeches off the neck and other exposed parts of skin (Player, 27.12.54).

In Borneo, sandpipers are reported to be similarly associated with *C. porosus* (Beccari, 1904; Hose, in Shelford, 1916).

While the commensal birds rid the crocodile of some ecto-parasites, these and other species play a far more important role in giving timely warning of danger. On countless occasions, while concealed in the hide, I have noted the reptile's immediate response to the alarm signal of birds which, of course, become aware of an approaching man or boat before their sleeping companions. The shrill call of a Spur-winged Plover or Water Dikkop is sufficient to send most of the crocodiles stampeding into the water, while others, often the largest on the beach, will delay their departure—raising their heads and looking for the cause of alarm, before following in retreat. Even the craning of a goose's neck, or the flurry of a sandpiper, provides a sufficient stimulus; and all the crocodiles are at once alert and ready to leave.

In the capacity of watch-dog, *H. spinosus* takes pride of place in Uganda. While other species fly from the grounds when alarmed, the plovers will often remain, fluttering over the reptiles' backs and uttering the urgent notes—"quick, quick, quick"—as though to ensure that their charges are awake. Curzon (1849) saw one of these plovers dash itself two or three times against the head of a sleeping crocodile that he had surprised at close range. Such behaviour might appear incredible, were it not known that under similar circumstances oxpeckers react in the same way towards the rhinoceros—even attempting to arouse an animal that has been shot (Cumming, 1850).

The Water Dikkop is another regular associate on the sunning beaches and breeding grounds, and, especially in the season when the crocodiles are covering their eggs, one or more pairs of birds are nearly always to be found in the vicinity. On Buvu Island in early November, 1952, Lester and I found only two crocodile

nests (hunters having been active in the area) : within 12 feet of one, and 13 feet of the other, a Water Dikkop was sitting on freshly-laid eggs. At the time of this discovery of a possible nesting association and synchronization of breeding cycles in the crocodiles and birds, I was unaware that Pitman (1950) had already noted the same phenomenon : he speaks of the birds' " definite association with crocodiles " and states that where the crocodiles breed there too will be found the eggs of *B. vermiculatus* " often . . . within a few feet of the brooding saurian." Player (7.2.55, 17.3.55) has observed the same habit in Zululand. It is not clear whether the partners derive mutual benefit from this nesting association. The birds undoubtedly serve the reptiles well as watchmen : it is also possible that from the habit of nesting beside the guardian crocodiles they may gain some adventitious protection against egg-eating enemies.

ECOLOGICAL STATUS

Population dynamics

The Nile Crocodile has no clearly defined mode of subsistence. Being a versatile opportunist, it maintains itself and meets varying circumstances with extreme flexibility of behaviour. Its ability to thrive, as an adult, upon prey ranging from crustaceans, molluscs and fish, to waterfowl, reptiles and large mammals, and upon carrion, gives it a unique status in its environment. Apart from the general role it plays as master predator, it occupies no single niche, but rather many niches—both on land and in the water. Thus it seems unlikely that food shortage can normally be an important factor in limiting its numbers. Should one food become temporarily scarce, the crocodile can turn to another, and in so doing it will exercise a differential pressure upon the shore and fresh water community. Moreover, the marked divergence in prey, feeding habits and habitat of young and old crocodiles—which is even more marked than that often found in a group of congeneric species (Gause's principle)—must tend to reduce intra-specific competition.

While the crocodile's place at the head of an elaborate system of food chains is unquestioned, heavy mortality, due to predation, nevertheless takes effect in the egg, newly-hatched young and adolescent stages. The maturing population also contains its own internal means of regulation, through cannibalism. Cannibalism also provides an explanation of the segregation of age-groups, for the habit tends to keep the young away from open water and basking grounds, in among weedy shallows.

In studies of the food habits of other animals, and especially of birds, attempts have often been made to evaluate the activities of particular species as " harmful " or " beneficial." The difficulties involved in attempting any such assessment have been discussed by Ritchie (1931) and Hartley (1948). The concept rests upon the assumption, rarely proved, that the predator is in fact a major factor in controlling the density of a prey species that is injurious, or useful, to agriculture, fishery or other other economic interests.

Even were it known that the crocodile exercised a controlling function upon the numbers of certain food organisms, it would not be possible to estimate its capacity for good or ill merely by comparing the proportion of "harmful" and "beneficial" food organisms eaten, when these are themselves so diverse in kind and habit, and so variously interconnected in a complex food web.

The web of food relationships in which the crocodile plays an essential part, is broadly outlined in Figs. 42 and 43, which indicate links in the chains: (a) which have been observed in the locality concerned (continuous lines); (b) which are known to obtain elsewhere (broken lines); and (c) which are unconfirmed but probable (dotted lines).

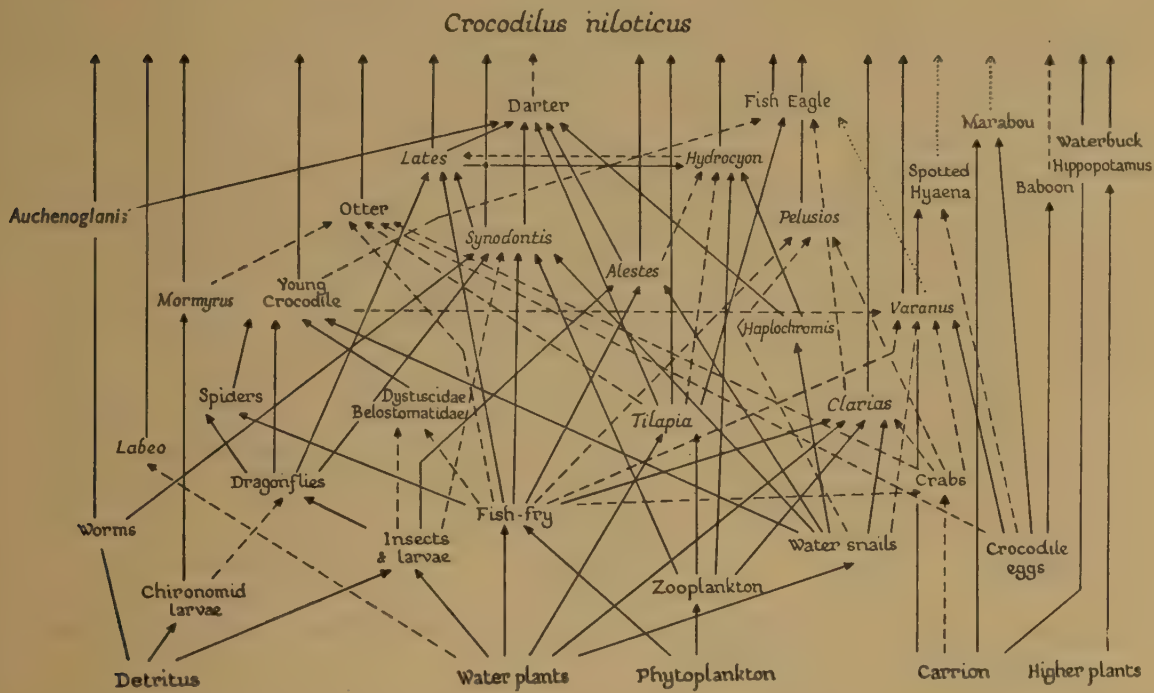


Fig. 42. Diagram showing the food relations of *C. niloticus* to various other members of the fauna : Uganda below Murchison Falls.

Examination of that part of the food web which primarily concerns reptiles and amphibia alone reveals sufficient complications, including cases of inter-specific competition and reciprocal predation. Thus, the turtle *Pelusios nigricans* and the monitor *Varanus niloticus* both feed extensively upon ampulariid gastropods such as *Lanistes* and *Pila*, which in some localities form a main item in the crocodile's menu at all ages. These three reptiles also prey upon the fresh water crab *Potamonautes*. Young crocodiles, and monitors, also eat toads and frogs, and the turtle takes tadpoles, while *Potamonautes* almost certainly includes anura in its generalised diet. Various snakes such as *Naia melanoleuca* and *Chlorophis hoplogaster*, themselves frog-eaters, are also preyed upon by the crocodile. The crabs and crocodile are both scavengers, readily feeding upon carcasses

including those of the crocodile itself. *Varanus* destroys crocodile eggs wholesale, also despoiling the nest of *Trionyx* and (presumably) of *Pelusios*. *Trionyx* is reputed to prey upon crocodile eggs and newly-hatched young. The crocodile in turn preys upon its enemy *Varanus*, and upon *Pelusios* and *Trionyx*: it also eats the eggs both of the turtles and of its own kind. And it rounds off these activities as a cannibal. Part of the food web is indicated in Fig. 44.

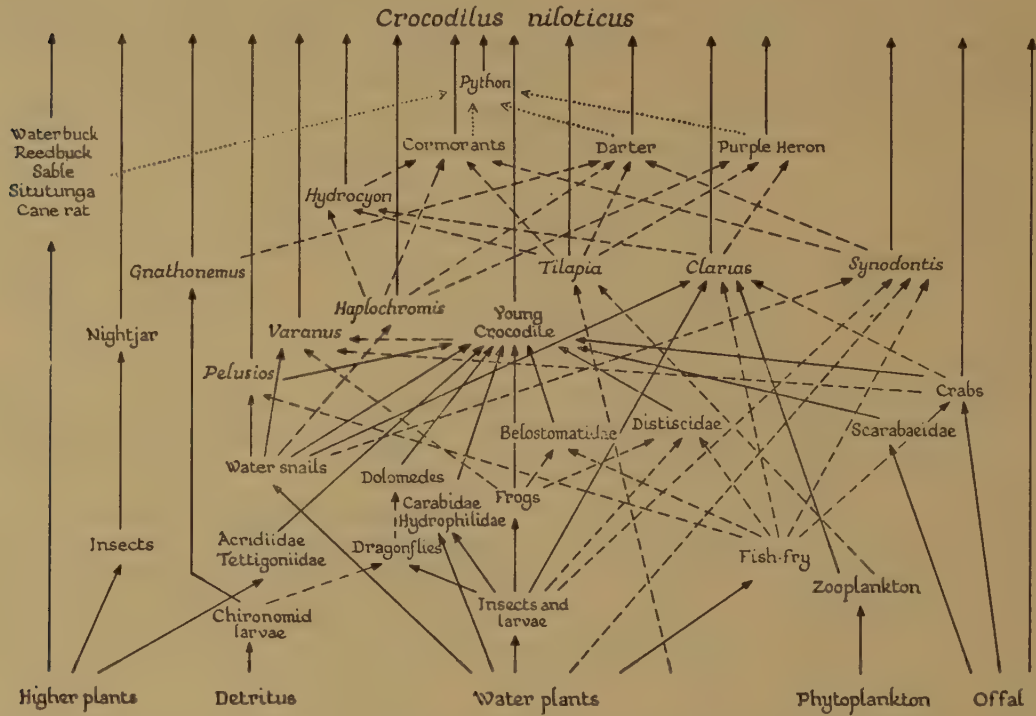


Fig. 43. Diagram showing the food relations of *C. niloticus* to various other members of the fauna : Upper Zambesi, Barotseland.

Similar complexities are seen at all levels of the food web. Thus, the feeding habits of young crocodiles reveal an intricate network of relationships—the reptiles preying extensively upon secondary predators such as belostomatid bugs and dytiscid and hydrophilid beetles, which in turn take tertiary predators such as dragonfly nymphs, young frogs and fish-fry. Young crocodiles also take pisaurid water-spiders whose victims include fish-fry and dragonflies—including *Crenigomphus rennei* and *Brachythemis leucosticta*—as observed at Kaiso, Lake Albert. These Odonata are themselves predatory upon other members of the insect fauna ; and the situation is further complicated by the crocodile's penchant both for larval and adult dragonflies.

In other food chains there are but two steps between the supply of plant material and the end-point—for instance, where herbivorous mammals form the intermediate link. But even where the predator's habits are thus simply defined, it is not easy to assess the effect upon the prey species. For predation is not necessarily harmful in its long-term effects, and indeed a predator may indirectly

benefit the species preyed upon—either by keeping the population in better adjustment to its own food supply, or by removing weakened or abnormal individuals. A dramatic example of the former effect is given by Leopold (1943) ; and examples of the latter by Rudebeck (1950) and Dobben (1952).

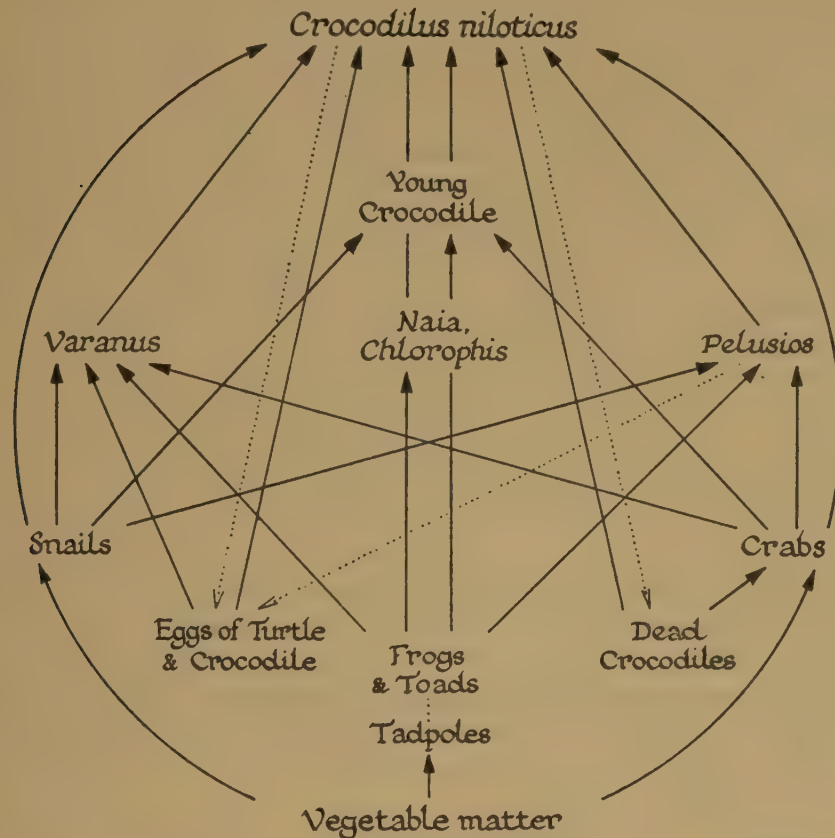


Fig. 44. Food relations of crocodiles to various other reptiles (see p. 317).

In this connexion, it is worth referring briefly to the crocodile's relation to the Hippopotamus in Uganda. Before the introduction of firearms, natural increase in the population was doubtless balanced by the activities of native hunters, by inter-male combat, and by the removal of old or injured individuals, and calves, by crocodiles. Today, under protection, the species has increased enormously in the Queen Elizabeth Park, and as a result over-grazing and land-erosion is evident over wide areas (Bere, 1955, 1959). The hippopotamus is also plentiful along the Victoria Nile in the Murchison Falls Park. But here no such excess has been reported. And it is perhaps significant—though quantitative proof is lacking—that these waters support a thriving population of crocodiles which are known to prey upon the hippopotamus ; whereas the Queen Elizabeth Park lacks this predator.

*Crocodiles and fisheries**Crocodiles and fish prey*

In most of the localities with which this investigation is concerned, comparatively worthless, or second-class fish (compared with the commercially desirable *Tilapia*, *Serranochromis* and *Sargochromis*) predominate among prey eaten. Only in Bangweulu Swamp were catches of *Tilapia* found to be in excess of other genera. In Lakes Kioga, Kwanja and Victoria, *Protopterus* and *Barbus* appear to be the main fish prey. Records from the Semliki River, Lake Albert and Murchison Nile indicate that *Synodontis*, *Alestes* and *Auchenoglanis* are the most important genera taken. Out of 119 fishes identified from stomachs in the Kafue and Zambesi Rivers, sixty-one were siluroids (*Clarias* and *Synodontis*): Jackson (27.1.58) informs me that this is certainly a higher proportion than occurs in the natural population. In Mweru Wa Ntipa crocodiles were found to be feeding almost entirely upon *Clarias*.

Several of the above-mentioned genera together with other fishes less often included in the diet—*Protopterus*, *Barbus*, *Clarias*, *Synodontis*, *Bagrus*, *Alestes*, *Hydrocyon*, *Lates* and various species of *Haplochromis*—are themselves at some stage predatory on fish, fry or fish-eggs. Thus it appears that the destruction of crocodiles would be unlikely to benefit fishery interests, and might well be harmful.

The wisdom of killing crocodiles in Hunyani Poort Dam, near Salisbury, has been questioned by L. H. Stewart, Secretary of the Natural Resources Board of Southern Rhodesia (Anon, 1952): and it was suggested that crocodiles should be maintained to limit the numbers of unwanted cannibal fish, such as barbel (*Heterobranchus*). Douglas Hey (*ibid.*), Director of Land Fisheries in the Union of South Africa, reported that where crocodiles had been reduced in the Belgian Congo, barbel rapidly multiplied.

Again, referring to the marked recent decline of crocodiles around Mwanza, Mr Lucas informs me (9.9.55) that the number of *Protopterus* appears to have increased, and that this is having an adverse effect upon the *Tilapia* fishery—as shown by the increase in the number of *Tilapia* mutilated in gill nets. R. S. A. Beauchamp (24.9.55) confirms that *Protopterus* mutilate fish in the nets.

Otters (*Lutra maculicollis*) are also causing an increasing amount of damage to netted *Tilapia* (E.A.F.R.O. Report, 1954–55) in Lake Victoria; and the destruction of crocodiles in Lake Mweru has also been followed by similar damage. The crocodile is known to prey upon the otter: two specimens, each bitten in half, were found in the stomach of a large crocodile in the Semliki River (Kinloch, 1951); and a freshly-killed specimen of *L. maculicollis* was recovered from a crocodile in the Kalungwishi River.

The importance of the crocodile in relation to the *Tilapia* fishery is clearly seen in the conditions at present obtaining in Mweru Wa Ntipa, where the reptiles are very plentiful and strictly protected. In this lake they tend to be monophagous, feeding extensively upon *Clarias mossambicus*, but apparently not upon *Tilapia*, which is the main producer of animal protein from vegetable matter,

and the important commercial fish. *Clarias* preys heavily upon *Tilapia*; and in so far as the crocodile keeps *Clarias* in check there can be little doubt that it is beneficial. If, owing to a change of policy, unrestricted hunting were to be permitted, crocodiles would speedily be exterminated, and the consequences might well be disastrous to the fishery.

Young crocodiles and invertebrate predators

On the evidence available, it is also reasonable to suppose that young crocodiles play a useful role in the fresh-water economy. During the early years of life crocodiles prey extensively upon giant waterbugs (Belostomatidae), adults and nymphs of dragonflies (Gomphidae, Libellulidae), voracious water beetles (Dytiscidae, Hydrophilidae), fresh water crabs (*Potamonautes*) and upon aquatic spiders (*Dolomedes*). All these invertebrates feed, either as larvae or adults, upon fish fry. Mr K. Morris tells me (21.5.54) he has on several occasions seen dytiscid beetles attack fry. Mr P. H. Greenwood tells me (15.12.56) that near Napoleon Gulf he has seen water spiders stalk and seize *Protopterus* fry as they surfaced. The Belostomatidae are formidable enemies; and here again the beneficial role of crocodiles may be presumed, especially in Uganda, where genera such as *Hydrocyrius* and *Limnogeton* are destroyed wholesale. The omnivorous crabs, which form an important part of the crocodile's diet in the Kafue and Upper Zambesi Rivers, also take their toll of fish: Mr A. D. Fraser informed me that in parts of Southern Rhodesia where crocodiles have been shot out of existence, crabs (*Potamonautes*) appear to have increased and are reported to be feeding in the nests of *Tilapia*. Fryer (1959) states that in Nyasaland *Potamonautes* "will readily feed on fishes entangled in gill nets—to which it sometimes causes considerable damage."

Crocodiles and fish-eating birds

Fish-eating birds, notably *Phalacrocorax lucidus*, *P. africanus* and *Anhinga rufa* play their part in the food web. In 1952 a large series of stomachs was examined in Uganda, and the following brief statement of results is relevant to the present discussion. Table 31 contains an analysis of prey, by genera, recovered from 246 of these birds which were shot in the same waters from which crocodiles were also examined. The figures in Table 32 provide a striking commentary upon the relative importance, as fish predators, of the birds and of crocodiles, respectively.

Bearing in mind the fact that crocodiles feed mainly upon fish only during part of their life-cycle and that even then many other foods are also taken, we are left with the surprising conclusion that the overall average daily fish-consumption of an individual crocodile is less in bulk than that of a White-breasted Cormorant (which consumes at least one kilogram of fish per day). Estimated in terms of occurrence, fish were found in only about one third of the crocodiles

which contained food of any kind : the birds are almost exclusively fish eaters. The mean number of fish per stomach is ten times greater in *P. lucidus* and *A. rufa* than in the crocodile. In the light of these observations, it must be remembered that cormorants and darters themselves constitute the main avian prey of the crocodile in most waters where the reptile's habits have been studied.

TABLE 31

Prey of White-breasted Cormorant, Pigmy Cormorant and African Darter, in Uganda—(a) Lake Victoria and Victoria Nile above Murchison Falls ; (b) Lake Albert and Victoria Nile below Murchison Falls.

	<i>P. lucidus</i>		<i>P. africanus</i>		<i>A. rufa</i>		Total
<i>Locality</i> No. of stomachs	<i>a</i> 87	<i>b</i> —	<i>a</i> 61	<i>b</i> 48	<i>a</i> 40	<i>b</i> 10	246
<i>Protopterus</i> ..	—	—	1	—	—	—	1
Mormyridae	11	—	—	—	1	3	15
<i>Hydrocyon</i> ..	—	—	—	2	—	—	2
<i>Alestes</i> ..	—	—	—	8	—	5	13
<i>Barbus</i> ..	4	—	—	1	—	—	5
<i>Labeo</i> ..	2	—	—	1	—	—	3
<i>Engraulicypris</i>	355	—	7	6	—	—	368
<i>Discognathus</i>	—	—	—	—	1	—	1
<i>Bagrus</i> ..	—	—	2	3	—	3	8
<i>Auchenoglanis</i>	—	—	—	2	—	1	3
<i>Clarias</i> ..	—	—	—	—	1	—	1
<i>Synodontis</i> ..	3	—	—	12	—	2	17
<i>Lates</i> ..	—	—	—	13	—	6	19
<i>Tilapia</i> ..	2	—	—	5	13	7	27
<i>Haplochromis</i>	398	—	139	159	293	47	1,036
<i>Astatoreochromis</i>	1	—	—	—	—	—	1
<i>Mastacembulus</i>	—	—	1	1	—	—	2
Total ..	776		363		383		1,522

TABLE 32

Comparison, in terms of occurrence and number of prey, of the fish-eating habits of water birds and crocodiles.

<i>Locality</i>	<i>Predator</i>	<i>Stomachs</i> containing food of any kind	<i>Stomachs</i> containing fish	<i>Per cent.</i> <i>stomachs</i> containing fish	<i>No. of</i> <i>fish</i> <i>prey</i>	<i>No. of</i> <i>fish prey</i> <i>per</i> <i>stomach</i>
Uganda	<i>P. lucidus</i>	87	87	100·0	776	8·92
Uganda	<i>P. africanus</i>	109	109	100·0	363	3·33
Uganda	<i>A. rufa</i>	50	50	100·0	383	7·66
	Total	246	246	100·0	1522	6·19
Uganda	<i>C. niloticus</i>	124	44	35·5	81	0·65
N. Rhodesia ..	<i>C. niloticus</i>	549	212	38·6	296	0·54
Zululand ..	<i>C. niloticus</i>	28	9	32·1	16	0·57
	Total	701	265	37·8	393	0·56

EXPLOITATION AND DECLINE

Causes of decline

In most parts of Africa where it was once abundant, *C. niloticus* has within recent years been drastically reduced in numbers. From wide areas the species has already vanished : from others it is fast disappearing.

Various factors have contributed to its decline. While the crocodile is affected by the general threat to all wild life which results from disturbance of natural habitats, its survival is also threatened more directly.

In the first place, the reptile suffers from a bad reputation, and is generally unpopular. It has never been scheduled as a species meriting protection under Game Laws ; but rather, has been officially classified as vermin. It is the only large animal for which permits are issued to regularise hunting by (otherwise) illegal methods of snaring, and shooting at night. In various territories campaigns have been authorised for its extermination. Thus for many decades, indiscriminate slaughter by every means available has been encouraged, in the supposed interests of humanity.

In more recent years the high profits to be made from hunting have led to a renewed and intensified onslaught, until in some territories the trade in belly-skins has become almost a major industry. Accurate figures for the toll taken are unobtainable, since there is a good deal of inter-territorial traffic—much of it by canoe, and by poachers. The following data (mainly based on the number of export permits obtained from the Department of Commerce) supplied by Mr D. H. Rhodes (23.5.56) give some indication of the crop taken from Uganda : 1953, 15,000 skins valued at £100,000 ; 1954, 7,900 skins valued at £44,553 ; 1955, 8,000 skins at £40,000. The value of the crop taken from other East African territories in the year 1954, as published in *East Africa and Rhodesia* (17 January 1957) was : £39,000 from Kenya, and £146,206 from Tanganyika. The number of crocodiles shot in East Africa that year was stated to be about 60,000. The report concludes with the laconic comment : “ In Kenya the numbers are falling and traders are alarmed.” Similar exploitation is taking place in Central Africa. For example, J. Nieuwoudt, a hunter operating in Northern Rhodesia, reported to the Department of Game and Tsetse Control (6.8.54) that between 1st January and 15th July, 1954, he handled a total of 5,721 skins, representing a turnover of about £20,000.

Modern hunting methods

The main immediate threat to the crocodile's survival comes from the techniques now employed by professional hunters. Working at night in fast motor boats, these men easily locate their quarry in the beam of a powerful spot-light, approach at speed, shoot at point-blank range, and gaff the dying animal before it can sink. Against this form of attack the crocodile has virtually no defence.

The crocodile population is especially vulnerable : (a) in waters that lack marginal swamps and lagoons difficult of access to the hunter ; (b) during the

dry season when the reptiles have returned from inundated areas to the main bodies of open water ; and (c) in the vicinity of breeding grounds where, after the disturbance of nesting females, the eggs are left an easy prey to monitors.

As a result of this irrational exploitation for immediate gain, the crocodile has been almost shot out of existence in many areas where it was once abundant (Cott, 1954 a ; 1957). Meanwhile, the hunters attempt to justify their activities on the grounds that they are performing a public service in eradicating a dangerous animal ; or they meet criticism with the contradictory assertion that the supply is inexhaustible.

The high prices paid for skins provide a powerful incentive to poachers. Working from canoes, and using snares or baited hooks, or harpoon and light in night operations, these men easily escape detection. And, as the supply fails elsewhere, the crocodiles that remain hitherto preserved in reserves and national parks offer an irresistible attraction. For example, Bere (1958) reports the disturbing news that commercial hunting has been a regular occurrence near and inside the Murchison Falls Park. The spectacular congregation of crocodiles at Magungu, which I had the good fortune to observe and photograph in the undisturbed state in 1956, has already been extirpated ; and Bere informs me (2.1.60) that native poachers have recently pressed home their attack upon the main headquarters of the reptiles at Fajao, below the Falls, and that numbers in this last stronghold in Uganda have been reduced.

Hunting and population structure

Since profits are related to belly-width of the skins, hunters shoot larger in preference to smaller crocodiles. Hunting is indiscriminate as regards the sexes which (except for the largest males) cannot be distinguished in the field. Hence the animals first sacrificed are the breeding stock of both sexes. Subsequently the smaller size groups—immature specimens and juveniles—are successively exploited. This process eventually includes crocodiles in their second and third year of life.

The changes in the depleted population which result from this traffic are apparent in every locality where commercial hunting has proceeded unchecked. For example, Mr P. H. Greenwood tells me (8.8.54) that in 1954 a Czech hunter, equipped with a large motor boat, a European assistant, two Sikh gunners, a crew of fourteen Africans and three powered canoes, accounted in six weeks for about 1,000 crocodiles in and around Buvuma Channel, L. Victoria. Very few of these were more than four feet in length. The average length of sixty shot in one night in Napoleon Gulf was again about four feet. Similar changes in the population structure are shown by a comparison of the length frequency distribution of reptiles, examined during the present survey, from waters : (a) which had previously been much shot over—Luangwa Valley and Kafue Flats ; (b) where hunting had been discouraged for a number of years—Upper Zambesi in Barotse-land : and (c) where crocodiles have hitherto enjoyed complete protection—Mweru Wa Ntipa (see Table 33 and Fig. 45).

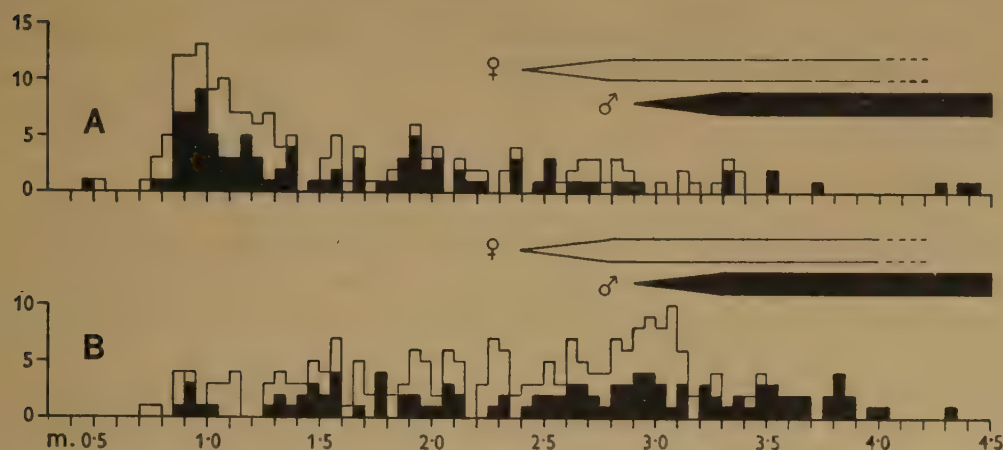


Fig. 45. Comparison of length frequency distribution of crocodiles shot : A—in areas where hunters had already been at work (Luangwa Valley and Kafue Flats) ; and B—in areas not previously exploited. The wedges indicate the onset of breeding maturity : black—males ; white—females.

TABLE 33

Showing the distribution, by sexes, of immature and adult crocodiles collected in four localities in Northern Rhodesia. The threshold for maturity is here based upon a length of 3.0 metres for males, and 2.5 metres for females.

Locality	Males			Females			Total			Mean length
	No.	Imm.	Ad.	No.	Imm.	Ad.	No.	Imm.	Ad.	
Luangwa Valley	55	55 100%	0 0%	39	34 87%	5 13%	94	89 95%	5 5%	1.54 m. (5ft. 0½ in.)
Kafue Flats ..	44	36 82%	8 18%	48	35 73%	13 27%	92	71 77%	21 23%	1.71 m. (5ft. 7 ins.)
Upper Zambesi	78	61 78%	17 22%	106	72 68%	34 32%	184	133 72%	51 28%	2.17 m. (7ft. 1½ ins.)
Mweru Wa Ntipa	31	9 29%	22 71%	20	0 0%	20 100%	51	9 18%	42 82%	3.18 m. (10ft. 5 ins.)

In Mweru Wa Ntipa, where crocodiles had not previously been hunted, 82 per cent. of the catch was of mature size, and the mean length was 3.18 metres (or about 10 feet 5 inches). Only 5 per cent. of the specimens taken in the Luangwa Valley were mature, and the mean length of the catch was 1.54 metres (or about 5 feet).

CROCODILE PROTECTION

Status in relation to man

Nothing has come to light from the present survey which would justify the classification of the Nile Crocodile as vermin. On the contrary, whether considered

from the point of view of ecology, economics or zoology, it is a valuable and important member of the African fauna.

Ecological status

On the ecological side, the conclusion may be reached that crocodiles are not detrimental to fishery interests, except in so far as, in certain localities, they damage gear. On the other hand, there is evidence that their presence is directly or indirectly beneficial to the industry.

In general, relatively few fish are eaten except in the middle years of life (see p. 294) ; and, in various localities, a large proportion of fish prey are either of secondary value or are predatory species (see p. 320). Juvenile crocodiles, representing the most numerous and voracious age group, account for many enemies of fish, fry and eggs (see p. 321). Adults take their toll of otters, cormorants and darters.

The reptiles also play their part as important scavengers of inland waters ; and on this account alone they merit the consideration that is accorded to vultures and Marabou which, as I am informed by Pitman (20.10.59), are protected by law throughout British Africa for their value as carrion feeders.

Finally, the specious argument that the Nile Crocodile merits persecution because it endangers human life will impress no one who is familiar with the species in the field today. Its depredations have often been grossly exaggerated, as by Hubbard (1927) and Siggins (1931). In all areas known to me in Uganda, Northern Rhodesia and Zululand, human fatalities appear, from inquiries made, to be rare. This conclusion is fully supported by the observations of Lang (in Schmidt, 1919) from the Belgian Congo.

Commercial status

There are two grounds for regarding the crocodile as a commercial asset. Firstly, it is a producer of high-quality leather. But hitherto intensive hunting has been carried out irrationally, on a mining rather than a cropping basis. Already in many parts of Africa the hunters and their agents are showing concern at the reduced yield. Under rational management, the reptiles could provide a sustained yield of skins to the trade. But if the industry is to be saved, it will be necessary to check the present uneconomic slaughter.

The species has a subsidiary, but by no means negligible value, as a tourist attraction. Speaking of game in general, Simon (1957) has stated : " Quite apart from any other consideration, the future of East Africa's tourist trade is irretrievably linked with our wild fauna. Visitors come from all over the world to observe and admire the unrivalled variety of wild animals, and as a result of this the Exchequer benefits to the tune of over six million pounds per annum. This ranks third in the list of revenue earners." To this end, crocodiles undoubtedly make their contribution.

Scientific status

Crocodylians also merit protection in their own right. Crocodiles essentially like the modern species existed in Jurassic times and were contemporaries of the dinosaurs. As the only remaining members of the archosaurian stock which have survived the age of reptiles, they are of quite exceptional scientific importance, not least from the indirect light which studies of anatomy, physiology, ecology and behaviour can throw upon the biology of ancestors long extinct. It would be a grave loss to science and research, and to posterity, if these saurians—which have survived for over a hundred million years—were now to be sacrificed to the demands of uninformed public opinion, and subordinated to a passing fashion in leather goods.

Conservation and control of hunting

The speed at which the Nile Crocodile is losing ground almost everywhere in Africa presents a challenging conservation problem that demands urgent attention. Intensive hunting, as at present practised, is taking toll of all sizes, young and old ; breeding stock, is being killed out ; and potential breeders are shot years before they would reach adolescence. The inroads now being made upon the population provide a classic example of exploitation and mismanagement of a valuable asset.

If conservation is to become effective, measures must be framed with regard : (a) to modern hunting procedure (see p. 323) ; and (b) to the slow growth of the crocodile (see p. 245). In waters where hunting has reduced the population down to young animals in their third and fourth year, the species needs a long rest—for a period of at least fifteen years.

To allow for recovery, complete cessation of commercial hunting is advocated. Half-measures, such as the prohibition of hunting at night, or the introduction of a close season, are likely to be ineffective because they could not be enforced over vast areas of difficult terrain. The ease with which poachers can evade detection is sufficiently illustrated by recent exploits of African harpooners who have been operating in the heart of the Murchison Falls Park.

Protection can best be achieved only by depriving the hunter of his market for a prescribed period—through control of the import and export of skins. Strong opposition to such measures can be expected from the traders, and from hunters, on the grounds of interference with their means of livelihood. But in this respect the crocodile hunter should be regarded no differently from the hunter who wishes to make a living by the sale of game-meat or rhinoceros horn or ivory.

The general problem of the Nile Crocodile's relation to man is a very old one : and in the Book of Job the question is asked : " Shall the bands of fishermen make traffic of him? Shall they part him among the merchants? " It is hoped that the authorities concerned will now reconsider this question in the light of recent events and research, and so take appropriate steps before it is too late to save this unique and valuable member of the African fauna.

SUMMARY

The results here reported and discussed are based upon observations of free-living crocodiles, and upon the examination of 576 freshly-killed specimens, during the years 1952, 1956 and 1957. The field observations mainly derive from the Murchison Falls National Park, Uganda. Study material was obtained in Uganda—from Lakes Victoria, Kioga and Albert, the Lower Semliki and Victoria Nile; and in Northern Rhodesia and Barotseland—from Bangweulu Swamp, Mweru Marsh, and the Luangwa, Kafue and Upper Zambesi valleys (pp. 215–217).

Studies in Uganda have shown that crocodiles observe a general diurnal rhythm of activity. The night is spent in the water. The haul out to land begins in the hour before sunrise. There are two main basking periods, between 0700 and 0930 hrs. and between 1430 and 1730 hrs. In the heat of the day there is a secondary return to the water, or into shade. Counts made at 15-minute intervals of crocodiles seen ashore and afloat throughout the day are considered in relation to environmental factors and to the reptiles' thermal requirements (pp. 217–224).

Cloacal temperatures of crocodiles shot at different hours of the day and night point to a remarkable degree of thermal control. The mean temperature is 25.6°C . with observed fluctuations from the mean of $+3.4^{\circ}\text{C}$. and -2.6°C . Records of diurnal movements and observations on the habit of mouth gaping, indicate that thermal control is effected both by habitat selection and behavioural adaptation (pp. 225–229).

The methods of locomotion on land are described. There are three distinct gaits: the high walk is the method of progression used when hauling out and in unhurried movement overland; the belly run is generally seen when the crocodile is making its escape downhill; the gallop has very rarely been observed and only in juveniles when surprised in sleep at close range. Crocodiles have exceptionally been encountered many miles from the nearest water; and in certain localities aestivation appears to be a regular dry season habit (pp. 229–232).

An account is given of aquatic behaviour. Swimming is effected by the tail, the limbs being closely applied to the flanks. Experiments with specimens restrained under water, and observations on diving times in free individuals, indicate that diving endurance increases with crocodile length. Specimens less than one metre long can remain submerged for at least 44 minutes; and the maximum dive for an adult is believed to be far in excess of the one-hour period that has been observed (pp. 232–235).

The occurrence and weight of stomach stones has been recorded for 507 crocodiles. Stones are first ingested at some period after the first year of life: they are invariably present in the adult. The growth stage at which the whole population becomes stone-bearing is considered in relation to habitat. The weight of stones increases with growth until maturity: adults of both sexes carry a mean standard load amounting to about one per cent. of the body weight. Strong circumstantial evidence suggests that stones are deliberately swallowed; and several classes of facts, which are discussed in detail, indicate that the stones subserve hydrostatic functions (pp. 236–245).

The available data on growth rate in wild and captive crocodiles are assembled.

Growth is most rapid in early life, showing a mean annual increment during the first seven years of about 10·4 inches (or 265 mm.). Thereafter the growth rate decreases progressively, to about 1·4 inches (or 36 mm.) per annum at twenty-two years of age. Records of exceptionally large crocodiles are given for East and Central Africa. The maximum size attained differs widely according to locality. On reliable evidence specimens appear to attain a maximum length of at least 20 feet. Longevity is discussed (pp. 245–251).

An even sex-ratio—324 males and 327 females—is recorded for the combined collections. The sexes are also about equal in the lower length groups. The changing constitution of the population as it ages is discussed. Sexual maturity is attained by the male at a length of about 2·9 to 3·3 metres, and by the female at a length of about 2·4 to 2·8 metres. Present knowledge of the growth rate indicates that females do not attain sexual maturity until they are at least 19 years old (pp. 251–258).

Observations made on the ovarian condition and on nest eggs show that the breeding season differs in different localities. Eggs are laid in Northern Rhodesia and Barotseland in September; in Lake Albert and the Victoria Nile below Murchison in early January; and in northern Lake Victoria in August and again in December. The relation of the breeding season to environmental factors is discussed. It is shown, in each locality for which data are available, that laying occurs when water levels are falling, that the incubation period coincides with the phase of lowest water, and that hatching takes place after the onset of the rains. The biological advantages of this synchronization are considered (pp. 258–266).

Large males are known to defend a territory, which may be a basking or feeding place. Little is yet known of territorial behaviour in the breeding season. The very unequal incidence of serious injuries found in the sexes indicates that inter-male rivalry finds expression in combat. Different kinds of vocalization are reported. Roaring by males has only been heard in the breeding season: the full roar, which may be a mating call, is described. An account is given of a pre-nuptial display in the female and of the preliminaries to copulation—which takes place in shallow water (pp. 267–269).

The requisite conditions for the nest site are discussed. Colonial nesting grounds on the southern shore of Lake Albert are described and it is suggested that the habit of breeding in colonies—today only seen where crocodiles are entirely free from disturbance—may formerly have been normal for the species. Data are given of clutch sizes: observations suggest that there may be a correlation between the number (but not the size) of eggs laid and the size of the parent. Earlier statements that the incubation period is about 90 days have been confirmed (pp. 269–275).

Throughout the incubation period the female guards the nest, either lying over the eggs or in nearby shade. At this time females may become torpid and reluctant to leave the grounds even when approached. The young croak as hatching time approaches: they cannot emerge until liberated. Eye-witness accounts, and the appearance of the shallow nest craters after hatching, indicate that the eggs are uncovered by shovelling movements of the parent's belly and not by the feet. An account is given of parental care of the newly-hatched young, and of the

crocodile's habits in early life (pp. 275-278).

A detailed account is given of the food and feeding habits, based upon field observations and upon the stomach contents of 851 crocodiles. It is shown that the diet is extremely varied, and that it changes markedly and progressively with the predator's age. The young feed in shallows and ashore on insects, spiders and frogs; in middle life underwater prey, notably crabs, gastropods and fish, form the main food; old crocodiles feed increasingly upon reptiles and mammals. Data are presented relating to the quantity of food eaten by wild and captive crocodiles. Prey organisms recovered from stomachs are tabulated systematically and in relation to localities. The crocodile's methods of hunting, capture and disposal of prey are described (pp. 278-303).

Among enemies that take a toll of the eggs, the Nile Monitor, *Varanus niloticus*, is far the most destructive. Other egg-predators include Marabou, *Leptophilos cruminiferus*, Water Mongoose, *Atilax paludinosus*, Spotted Hyaena, *Hyaena crocuta*, and Olive Baboon, *Papio anubis*. Records of predation upon newly-hatched young are briefly reviewed, and instances are given of attacks upon adults by hippopotamus and elephant, and of predation upon adults by lion and leopard (pp. 304-306).

Data relating to the occurrence, site and nature of external injuries are recorded for 548 crocodiles examined. Injuries are more frequent in older than in younger animals, and in males than in females. Evidence is given to suggest that most injuries result from the habits of cannibalism and inter-male combat. Particulars of more or less disabling wounds and amputations in twenty-seven specimens are tabulated (pp. 306-309).

In Uganda the tsetse-fly *Glossina palpalis* is a common parasite of the crocodile. Reference is made to blood parasites transmitted by the fly. Crocodiles are frequently infested with leeches—*Placobdella fimbriata* in Uganda and *P. jaegerskioeldi* in Northern Rhodesia. Data relating to occurrence, site and degree of infestation are given for 506 crocodiles. Infestation tends to increase progressively with age, first-year crocodiles being entirely free of these parasites. Nematodes, which include *Multicaecum agile* and *Dujardinascaris dujardini*, were found in forty-four stomachs in a sample of sixty-six examined in Uganda (pp. 310-313).

Birds of many kinds, including darters, herons, egrets, duck, dikkops, plovers, waders, pratincoles, skimmers and wagtails, frequent the basking grounds. Crocodiles tolerate their presence and react to their alarm signals. Such fortuitous relationships grade into those of true commensalism, which have been observed in the Spur-wing Plover (*Hoplopterus spinosus*), Common Sandpiper (*Actitis hypoleucos*) and Water Dikkop (*Burhinus vermiculatus*). The relations between these birds and the crocodiles are described. In Uganda, *H. spinosus* and *B. vermiculatus* habitually feed on the grounds and give the reptiles timely warning of danger. In Uganda and Zululand *A. hypoleucos* has been observed ridding crocodiles of ectoparasites. And from both localities there is evidence of a nesting association between *B. vermiculatus* and *C. niloticus* (pp. 313-316).

The status of the crocodile in the bionomics of inland waters is discussed. The young are shown to be ecologically separated from the adults. Attention is drawn to the complex web of food relationships in which *C. niloticus* plays a part as

master predator, cannibal and scavenger. The crocodile's relation to commercial fisheries is considered. The young feed extensively upon belostomatid bugs, dragonflies, dytiscid and hydrophilid beetles, and crabs—all of which prey upon fish fry. In most localities with which the investigation is concerned, a large proportion of the fish prey of adults are either comparatively worthless or predatory species. The relations between crocodiles and fish-eating birds is discussed. Various harmful effects, apparently resulting from crocodile destruction, are noted (pp. 316–322).

The Nile Crocodile has within recent years been drastically reduced in numbers : the causes of its decline are reviewed. The main immediate threat to its survival comes from modern methods employed by professional hunters. Examples are given of the effect of hunting upon the population structure. The reptile's status in relation to man is reassessed. Evidence is given to show that from the points of view of ecology, economics, and zoology, *C. niloticus* is a valuable member of the African fauna. Recommendations are made for its conservation (pp. 323–327).

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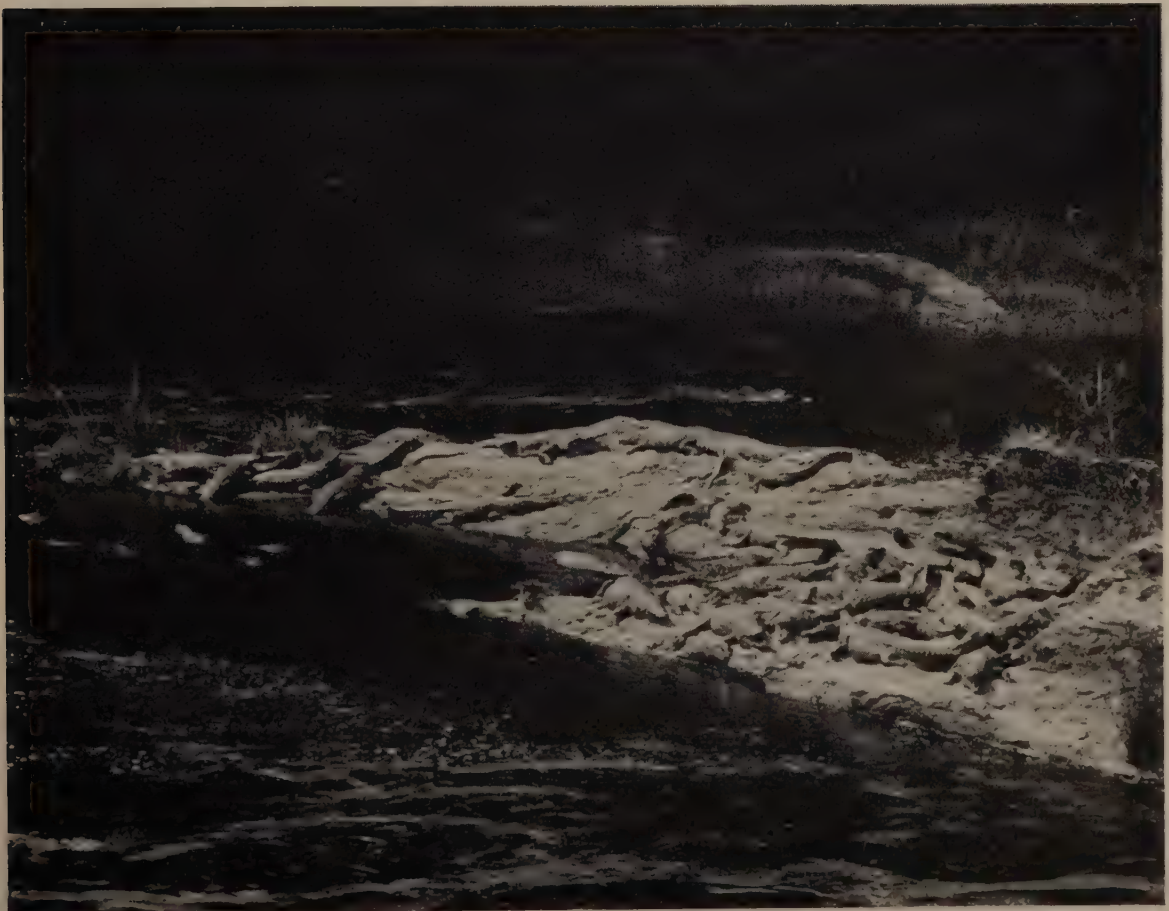
PLATE 1

PLATE 1

- Fig. 1. Congregation of crocodiles on the grounds at Magungu, Victoria Nile. The reptiles have become aware of the approach of a launch. Several can be seen in the typical alert attitude, with head raised and tail flexed. One, in the centre, is leaving at the high walk. Two, in the foreground, are already afloat. July 1952.
- Fig. 2. A sector of the rock islet below Murchison Falls, as seen from Murchison Observation Post. The photograph shows twenty-three large crocodiles basking ashore, many with the jaws widely gaping ; five lie partly in the water, with the tail trailing. Several others can be seen floating in the lee of the rock, and one is keeping station in the rapid current. 12th July, 1956.



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2

PLATE 2

PLATE 2

- Fig. 1. A crocodile has left the water to bask in the early morning sun. Note the closed jaws. Near Paraa, Victoria Nile. 5th July, 1956.
- Fig. 2. Lateral study, at close quarter, of a mouth gaping crocodile. Several tsetse flies, *Glossina palpalis*, can be seen feeding between the scales on the head and jaws. Near Nansika con-fluent. 5th July, 1956.



1



2

The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 3

PLATE 3

- Fig. 1. The crocodile in the centre has just emerged from the river, and laboriously hauls itself up the beach. The belly is raised high off the ground : the hind limbs bear most of the weight while the fore limbs serve as props to support the head and shoulders. The animal photographed is about to swing forward the left hind and right fore limbs, while the weight is carried on the opposite diagonal pair. Magungu. 31st December, 1956.
- Fig. 2. Photograph showing the belly run, which is the gait normally adopted when the crocodile is hastily seeking refuge in the water. These reptiles have been alarmed and are tobogganing downhill at speed. The limbs are splayed sideways and used as oars. Murchison. 25th July, 1956.



1



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The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 4

PLATE 4

- Fig. 1. A crocodile has just taken to the water and is seen cruising. Only the nasal disc, top of the head, and mid dorsal scutes appear above the surface. Note the flexure of the tail, which alone drives the animal forward : the limbs are applied to the flanks and take no part in propulsion. Paraa. 26th July, 1956.
- Fig. 2. The most powerful demonstration of a crocodile's vocal repertoire is the full roar, which is often heard in the breeding season. The photograph shows a large male in the act of roaring. It is looking across the river, its gular shields raised high off the beach, with head inclined upwards and jaws widely gaping. Magungu. 31st December, 1956.



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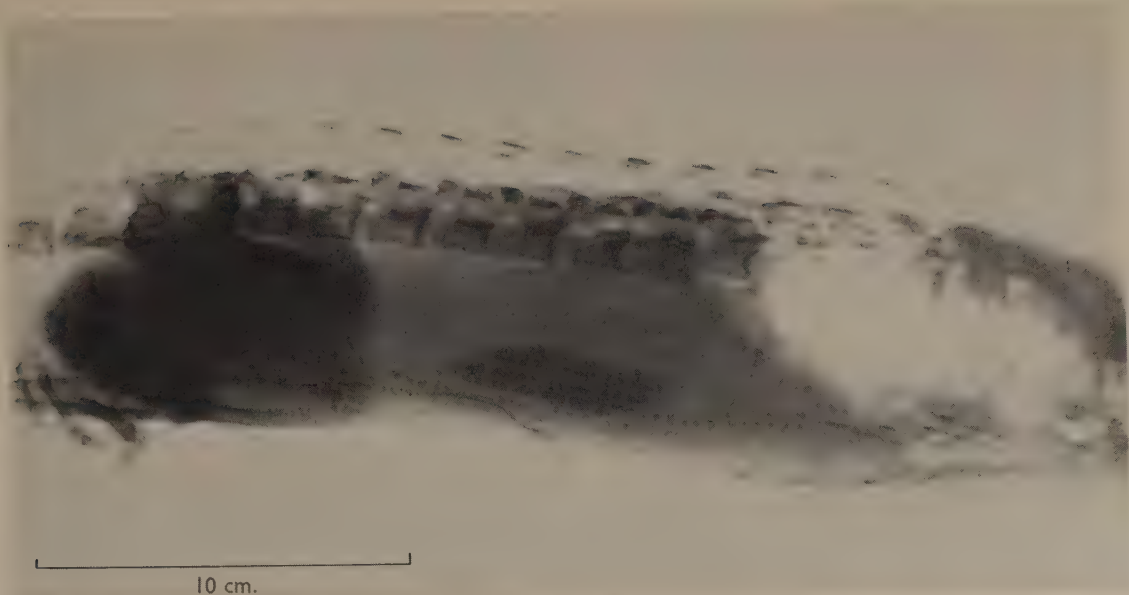
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The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 5

PLATE 5

- Fig. 1. X-ray (lateral view) of a specimen measuring 1.1 metres (total length) showing the position of stomach stones low in the body.
- Fig. 2. The same (vertical view). The author is indebted to Mr B. L. Mitchell (Department of Game and Tsetse Control) who supplied the negatives, and to Mr J. A. F. Fozzard (Anatomy School, University of Cambridge) who prepared the prints.



1



2

The Nile Crocodile in Uganda and Northern Rhodesia.

PLATE 6

PLATE 6

- Fig. 1. Head of crocodile No. 193, a male measuring 3·38 m. total length, showing abnormality of snout resulting from serious injury. Mweru Wa Ntipa. 15th September, 1956.
- Fig. 2. Crocodile No. 27, a female measuring 3·12 m. total length, showing site of amputated fore-limb, with pad of regenerated scales. Ripon Falls. 8th July, 1952.
- Fig. 3. Head of crocodile No. 124, a male measuring 2·55 m. total length, showing amputation at lower jaw, healed injury, and recurved anterior teeth of upper jaw. Bangweulu Swamp. 23rd August, 1956.
- Fig. 4. Head of crocodile No. 190, a male measuring 2·86 m. total length, showing amputation at lower jaw, dental abnormalities, and clusters of leeches in dental sockets. Mweru Wa Ntipa. 14th September, 1956.



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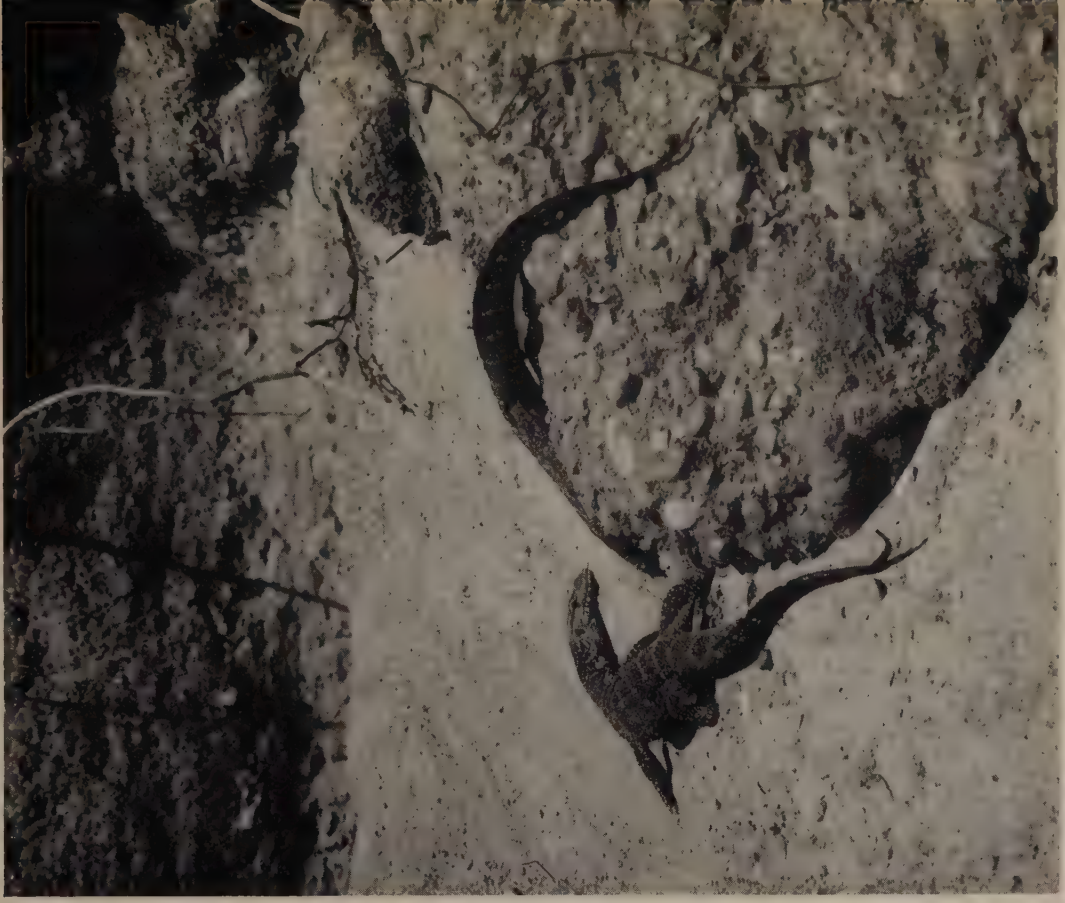
PLATE 7

PLATE 7

- Fig. 1. Female guarding her nest on a steep river bank site, about fifteen feet above the water. Near Paraa. 27th December, 1956.
- Fig. 2. The same site after the female had been disturbed. Two Nile Monitors, *Varanus niloticus*, are seen searching for the eggs. 8th January, 1957.



1



2

PLATE 8

PLATE 8

- Fig. 1. The photograph shows a basking crocodile closely attended by a monitor, with an Egyptian Goose nearby. The monitor is one of several which frequented the Magungu grounds, and which in the breeding season were constantly searching for eggs of *C. niloticus* and *Trionyx triunguis*. 31st December, 1956.
- Fig. 2. Typical early morning scene on the Magungu grounds. Several large crocodiles are ashore, some lying across the bodies of their companions. 4th August, 1956.



1



2

PLATE 9

PLATE 9

- Fig. 1. The Spur-winged Plover, *Hoplopterus spinosus*, is a constant companion of the crocodile at Magungu. Three of the birds are seen close to the gaping jaws of an animal in the foreground. 31st December, 1956.
- Fig. 2. Another typical scene on the Magungu grounds. The large crocodile in the centre is lying with the tail trailing in the water and with jaws agape. On the right a crocodile is cruising inshore prior to hauling out on the beach. The animal on the left is attended by a Spur-winged Plover, and a Common Sandpiper is seen close to the tail. 1st January, 1957.
- Fig. 3. A large male looks across the river from the Magungu grounds, while a Common Sandpiper takes a tsetse fly or leech from the base of the tail. 30th December, 1956.



1



2



3

The Post-notochordal Tail in Dipnoi and Urodela

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(With 3 plates and 16 figures in the text)

A post-notochordal tail always develops in the dipnoans *Lepidosiren* and *Protopterus*. It is sometimes present in Urodela where it occasionally attains a length and complexity comparable to that in Dipnoi. It develops when the notochord or vertebral column fails to extend posteriorly at the same rate as the nerve cord. After the post-notochordal rod has formed beneath the nerve cord and separated into caudal cartilages, the latter tend to be intersegmental and the joints segmental. Though similar in structural type to those of the notochordal region, the post-notochordal vertebral arches, nervous system, muscles and myosepta are subject to many aberrations, and segmentation is confused.

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INTRODUCTION

The purpose of this paper is to give an account of the structure and development of the dipnoan post-notochordal tail by reference to *Lepidosiren* and *Protopterus* and to show that a similar post-notochordal tail is developed in Urodela.

When Gunther described *Neoceratodus* in 1871, he stated that the notochord terminates abruptly at a considerable distance from the end of the tail and that neural and haemal arches are continued beyond the end of the notochord. He figured these post-notochordal elements correctly as situated on a jointed axis of caudal cartilages. These cartilages somewhat resemble vertebral centra and he thought that they were simply formed in the absence of the notochord by fusion of the bases of the arches. There is a similar arrangement beyond the end of the notochord in *Lepidosiren* and *Protopterus*.

Later descriptions of the skeleton in recent Dipnoi, e.g. Wiedersheim (1880), Hasse (1893), Klaatsch (1893), Gaddow and Abbot (1895), Schauinsland (1905), Kisselewa (1928) and Remane (1936) give practically no further information on the post-notochordal region but Remane, showing Klaatsch's figure of a post-notochordal skeleton in *Neoceratodus*, states that the caudal cartilages, though comparable to centra of vertebrae, do not bear a relationship to segmentation.

Budgett (1899) stated that during the breeding season the limbs and tip of the tail in *Protopterus annectens* become much elongated and attenuated. In this species the tail also becomes much reduced before and during aestivation in cocoons (see Blanc, d'Aubenton and Plessis 1956). Holmgren (1928) described the external appearance of the growing tip of the tail in two aquarium specimens of *Lepidosiren*. He showed that the growth of the dorsal and ventral caudal fin-webs did not keep pace with the elongation of the body stem. This resulted in a slightly three-lobed condition at the end of the tail with the body stem forming the middle lobe and turning slightly upwards. Despite the fact that the tail is normally much straighter and not trilobed in embryonic or young *Lepidosiren*, he thought that this growth stage resembled the tail in extinct crossopterygians.

It was not until 1930 that Miller, in a short paper, gave an account of the early development of the post-notochordal cartilages in young *Lepidosiren* and a 96 mm *Protopterus*. She proved conclusively from sections that the cartilages are truly post-notochordal in origin and arise from connective tissue behind the notochord. She found that the cartilages begin to form in larval *Lepidosiren* at approximately stage 31 (for stages see Graham Kerr 1900) and she showed that caudal cartilages develop behind the notochord and beneath the nerve cord when the nerve cord grows back beyond the end of the notochord.

When Mookerjee (1930) described the development of the urodele vertebral column, he did not mention the post-notochordal region.

Regenerated tails of urodele larvae are always post-notochordal. In contrast to the Anura, the notochord does not regenerate, and post-notochordal cartilage forms beneath the regenerating nerve cord (see Holtzer, Holtzer and Avery 1955, Holtzer 1956).

MATERIAL AND METHODS

Investigations were made on eighty specimens of *Protopterus aethiopicus* from Lake Victoria of which thirty, selected for detailed study, ranged from 92 to 380 mm in length, twelve specimens of *P. amphibius* (Trewavas 1954) 18 to 401 mm long and twelve specimens of *Lepidosiren paradoxa* 16 to 70 mm long. Urodela examined included *Amblystoma tigrinum* (white variety), *Triturus cristatus*, *vulgaris* and *helveticus*, together with other urodeles, Anura and Coecilia.

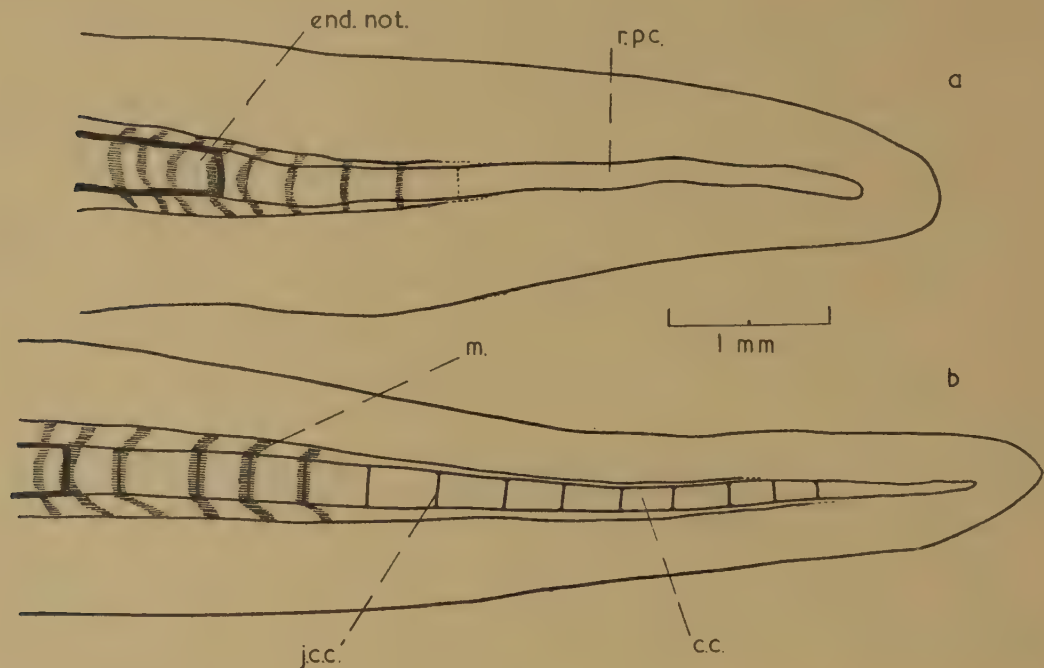


Fig. 1. *Lepidosiren paradoxa*. a. 32 mm; b. 39 mm.

c.c. caudal cartilage; end. not. end of notochord; j.c.c. joint between caudal cartilages; m. myomere; r.p.c. rod of post-notochordal cartilage.

The material was fixed in formalin or Bouin's fluid, decalcified in Jenkin's fluid and cleared in chloroform, which did not harden the tissues and diffused out rapidly during wax impregnation. Alternatively, tissue was transferred to diethylene dioxide and calcium oxide where it could be kept permanently. Nearly all the sections were 10 microns thick.

Among the stains used (see Plates 1-3) iron haematoxylin-ponceau S (Sharpey-Schafer 1954) was best for showing myosepta and nerves, and azocarmine-Mallory (Pantin 1948) was not satisfactory with formalin-fixed material. Whole preparations of the body or tail of dipnoans were made by staining in methyl green (Lundvall 1905) or Mayer's haemalum. They were cleared in benzene followed by oil of wintergreen. Some urodele tails were stained in borax carmine and mounted in balsam. Hydrogen peroxide was used for bleaching. Alizarin preparations (Gray 1929) were also made.

After drawing by projection, reconstructions were made from serial sections in the form of wax models (Norman 1923) or on tracing paper or on glass.

The total length from snout to tip of tail is given in the specimens described below but there is considerable variability in the degree of development of the post-notochordal region among individuals of the same size. The consignment of *P. aethiopicus* came from Lake Victoria and it is unlikely that this population aestivates in cocoons (Greenwood 1955).

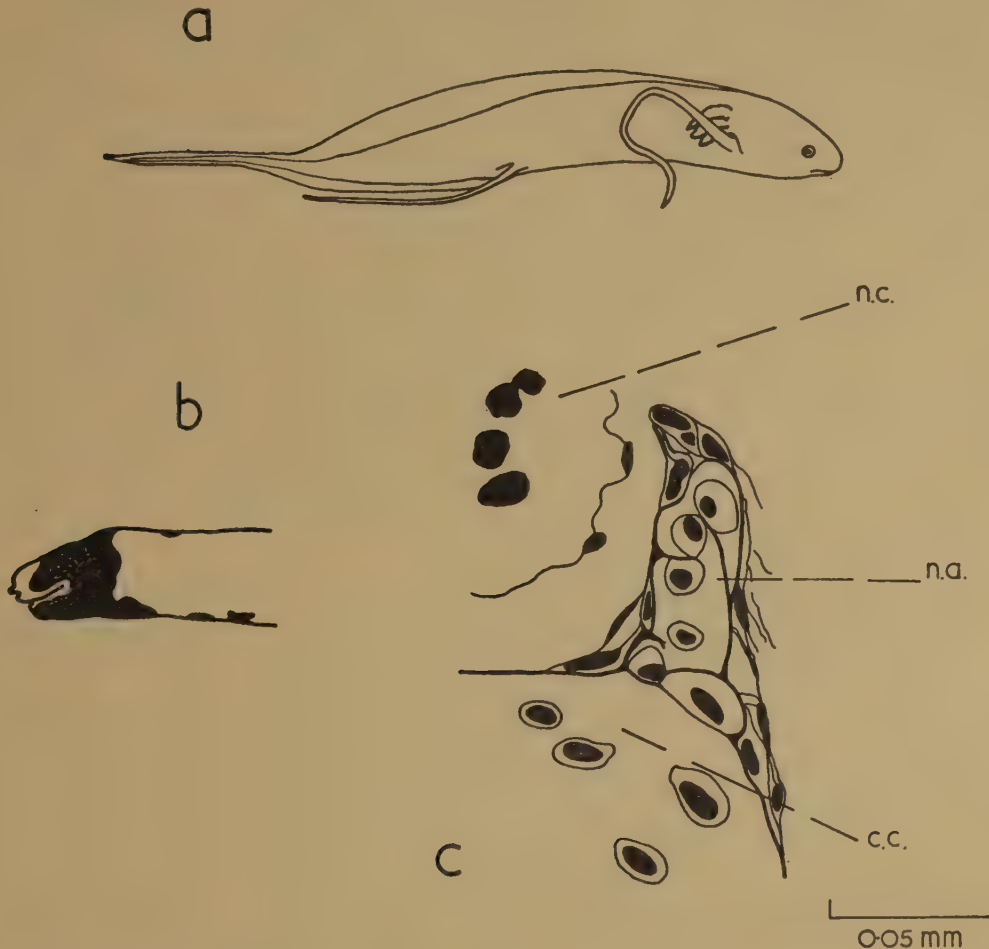


Fig. 2. *Protopterus amphibius*. a. 40 mm. b. Tip of tail more highly magnified. c. 85 mm, transverse section showing early stage in formation of post-notochordal neural arch. c.c. caudal cartilage; n.a. neural arch; n.c. nerve cord.

YOUNG *LEPIDOSIREN* AND *PROTOPTERUS*

In a 32 mm *Lepidosiren* there is a rod of cartilage behind the notochord (Text-fig. 1a), in which joints are beginning to form anteriorly. In a 39 mm specimen almost the entire rod, except at its posterior end, has become divided into separate caudal cartilages (Text-fig. 1b). Post-notochordal myomeres are differentiating alongside the joints.

Young *Protopterus* are not transparent like young *Lepidosiren*. The posterior part of the tail is very filamentous (Text-fig. 2). The extreme tip is nearly always frayed and there is no fin-web around it. In an 18 mm specimen the post-notochordal rod is 2.5 mm long and is circular in transverse section. The beginnings of fourteen joints along its length divide it into individual caudal cartilages. The cells forming the joints (Text-fig. 3b and c) can be distinguished from the cartilage cells proper (Text-fig. 3a and d) because they remain close together and do not lay down cartilage. Five post-notochordal myomeres have formed alongside the joints and there is a nerve cord, caudal artery and vein.

Sagittal sections from a 40 mm specimen show that the end of the notochord terminates on the convex anterior face of the first caudal cartilage. The primary sheath of the notochord fades imperceptibly into the matrix of the cartilage. Joints between caudal cartilages have become well defined (Text-fig. 3f). Sections from a 42 mm specimen with a twelve-jointed 7 mm post-notochordal rod show the anlagen of a pair of spinal ganglia (Plate 1, fig. 6), on either side, lying dorsal to the anterior caudal cartilage. Dermal fin-rays have also appeared.

In a 71 mm specimen the anterior face of the first caudal cartilage has expanded into the vacuolated tissue of the notochord (Plate 1, fig. 2) and cartilaginous arches are growing up around the nerve cord on several of the anterior caudal cartilages. The arches are dorsally incomplete and separate pieces of cartilage forming neural spines lie above them. There are no ventral arches but traces of haemal spines are present. Several post-notochordal ganglionic anlagen lie above the caudal cartilages and between the arches. Scales are now present in the post-notochordal region.

Sections from an 85 mm specimen show how the post-notochordal arches originate. The perichondrial connective tissue adds cartilage to the dorsal surface of the first caudal cartilage so as to expand it upwards on either side of the nerve cord (Text-fig. 2c). The neural arch is incomplete and there is no roof of cartilage above the nerve cord. There are no haemal arches. The anterior caudal cartilage is no longer round in transverse section, being much wider in the vertical plane than in the horizontal. This is shown in a larger specimen (Plate 1, fig. 7).

Neural and haemal arches are complete in the anterior part of the post-notochordal region of a 111 mm specimen and there is no suture line between the caudal cartilages and the bases of the arches (Plate 1, fig. 5). The neural arches have grown up around the nerve cord and fused with their respective neural spines. Growing downwards from the caudal cartilages, haemal arches have formed similarly to neural arches and have fused with their haemal spines. Dorsal and ventral basals and radials are present, and all the elements of the skeleton, except for the bases of the arches and the caudal cartilages, are covered by a thin layer of bone.

STRUCTURE OF THE TAIL IN *PROTOPTERUS*

The elements of the skeleton are arranged in a regular manner in the anterior notochordal part of the tail (Text-fig. 4). Situated dorsally in each myoseptum there is a neural arch, to which a neural spine is fused, a basal and a radial.



Fig. 3. Sections through the post-notochordal tail of *Protopterus*. *P. amphibius*, a-d. 18 mm; f. 40 mm. *P. aethiopicus*, e. 105 mm.
 a and d transverse sections through caudal cartilages. b and c transverse sections through joints between caudal cartilages. e, horizontal section through imperfectly formed joint. f, median sagittal section showing joint between caudal cartilages with nerve cord above and caudal artery beneath.

Ventrally in each myoseptum there is a haemal arch to which a haemal spine is fused, a basal and a radial.

In the post-notochordal region and to a limited extent in the region just anterior to the end of the notochord (Text-fig. 5) considerable irregularities occur. Many of the arches appear as composite or double structures. Occasionally there may be two quite distinct neural arches upon a single caudal cartilage. The haemal

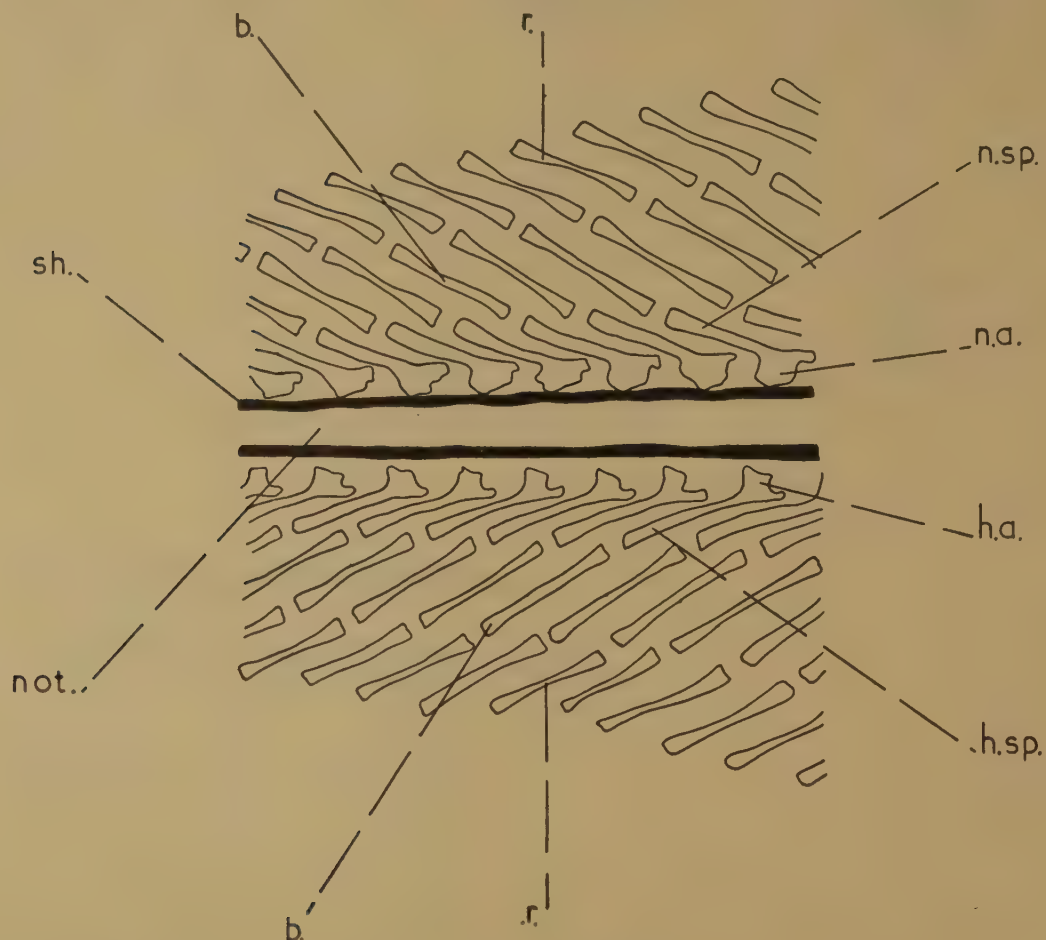


Fig. 4. Tail skeleton of *Protopterus* from an alizarin preparation.

b. basal; h.a. haemal arch; h.sp. haemal spine; n.a. neural arch; not. notochord; n.sp. neural spine; r. radial; sh. notochordal sheath.

arches tend to be more irregular and less distinct than the neural arches. Frequently additional struts or spines develop, and irregularities in the arrangement of the radials and basals make it impossible to say which of the two kinds of elements is represented (Plate 1, figs. 8 to 10). More posteriorly the arches are almost completely fused together, the nerve cord and caudal blood-vessels being surrounded by cartilage except for small apertures from which the nerves or blood-vessels emerge.

Fibrous pads are developed in fully formed joints between caudal cartilages and cavities may occur in the caudal cartilages (Plate 1, fig. 3). Near the tip of the tail, fibrous pads are absent and the joints are indistinct. Occasionally, a joint between caudal cartilages may be imperfectly formed. Where this was so, the specimen was not included in Table 1 (see below). In an imperfect joint, the joint cells only partially bisect the cartilage (Text-fig. 3e). Fibrous pads develop in the imperfect and perfect joints alike.

Some measurements from twenty specimens of *Protopterus* are shown in Table 1. The sample is not as large as could have been wished for and it may not be an entirely random one, because damaged tails, which are very common, were deliberately not included. Tails which might have regenerated (see Brindley 1900) were also excluded.

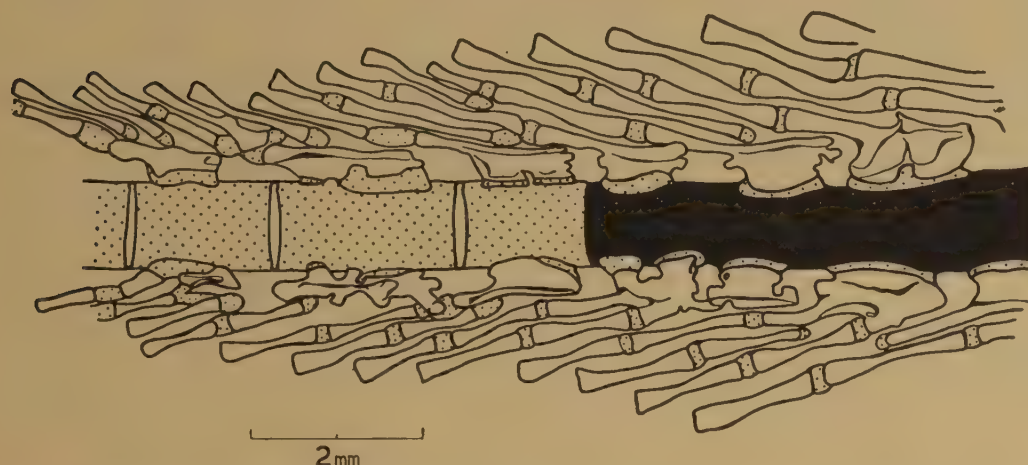


Fig. 5. Part of tail skeleton of an 185 mm *Protopterus aethiopicus*, from an alizarin preparation. Cartilage dotted, notochord black, bone and joints between caudal cartilages unshaded.

In each specimen the length of the whole tail L3 and the length of the post-notochordal region of the tail L4 are each expressed as a percentage of the total length L1 of the fish. Text-fig. 6 shows that in contrast to the relative length of the whole tail which is fairly constant, the relative length of the post-notochordal region is extremely variable, ranging from thirteen to thirty-seven percent of the total length of the fish. This variability is nearly five times as great as the variability in the relative length of the whole tail.

Text-fig. 6 may suggest that the length of the post-notochordal region is more variable in the smaller specimens. It would be necessary to take a much bigger sample before this could be confirmed. Nothing can be said of the age of the sample, except that as a whole, it must be composed of relatively young individuals. The members of the species have been recorded as reaching a length of 2 metres and most specimens caught by commercial fishermen range from 100 to 130 cm in length (Greenwood 1955). In larger specimens the tail is not nearly so attenuated and the post-notochordal region has not been studied.

TABLE 1. MEASUREMENTS FROM TWENTY *Protopterus aethiopicus*

Number	Total length	Snout to vent	Tail (vent to tip)	Post notochordal length			Number of caudal cartilages
				L1 mm.	L2 mm.	L3 mm.	
1	92	47	45	23	49	25	27
2	97	48	49	30	50.5	31	29
3	107	54.5	52.5	16	49	15	14
4	134	68	66	18	49	13	23
5	137	71	66	29	48	21	30
6	140	67	73	30	52	21	27
7	149	67	82	39	55	26	26
8	150	79	71	33	47.5	32	32
9	150	80	70	23	46.5	15	23
10	155	73	82	58	53	37	42
11	176	81	95	46	54	26	27
12	185	95	90	35	48.5	19	27
13	194	100	94	40	48.5	20	22
14	227	106	121	62	53.5	27	31
15	239	117.5	121.5	52	51	22	23
16	266	120	146	72	55	27	36
17	268	130	138	64	51.5	24	33
18	271	141	130	62	48	23	28
19	277	131	146	65	52.5	23	35
20	350	174	176	81	50.5	23	37

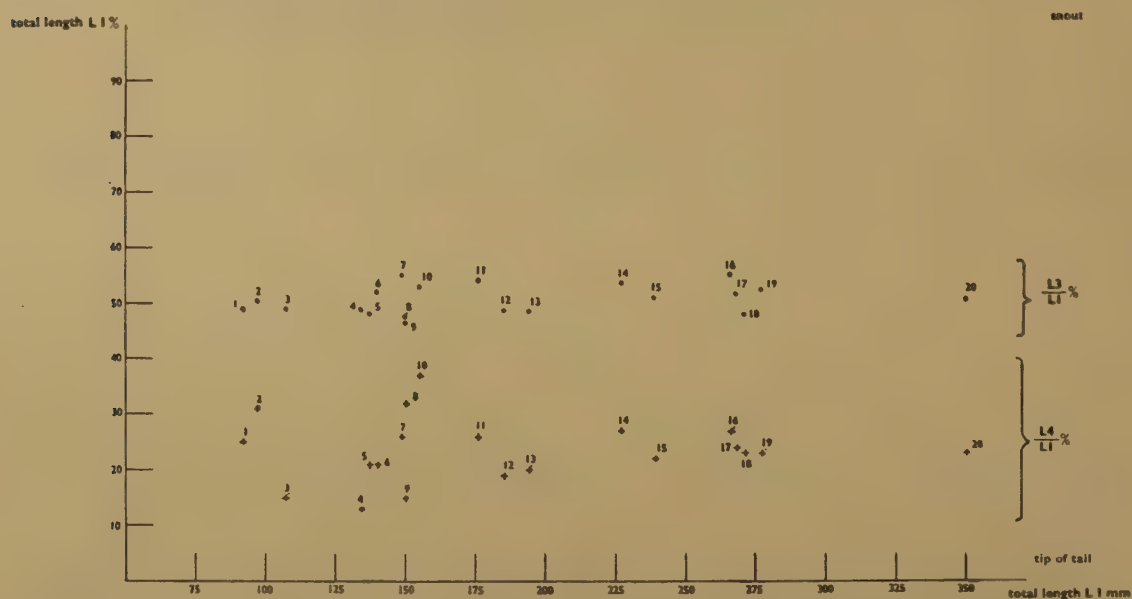


Fig. 6. Variations in the length of the whole tail and the length of the post-notochordal region of the tail expressed as per cent of the total length of the specimen in twenty *Protopterus aethiopicus*. In each case a dot denotes the position of the vent and a cross the position of the end of the notochord. The numbers against these points refer to the specimen numbers in Table 1. Standard deviation/mean value of $L3/L1=0.051$. Standard deviation/mean value of $L4/L1=0.25$.

There is great variability in the number of caudal cartilages in different tails. Nos. 3, 4 and 9 in Table 1 all have poorly developed post-notochordal regions but whereas No. 3 has only fourteen caudal cartilages, Nos. 4 and 9 each have twenty-three.

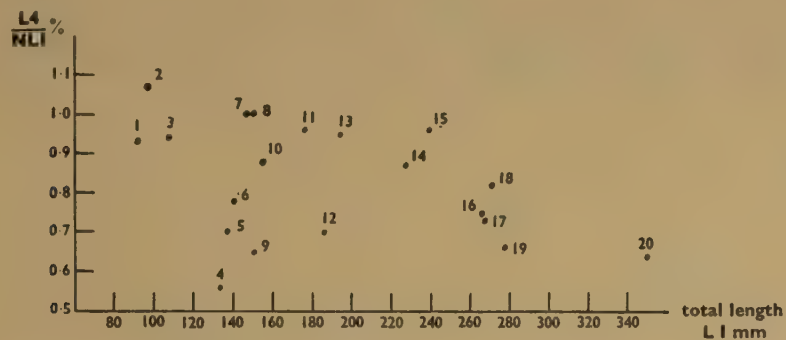


Fig. 7. Mean caudal cartilage length expressed as fraction of total length of specimen plotted against total length in mm in twenty *Protopterus aethiopicus*. The numbers against the points refer to the specimen numbers in Table 1. $r=0.78$.

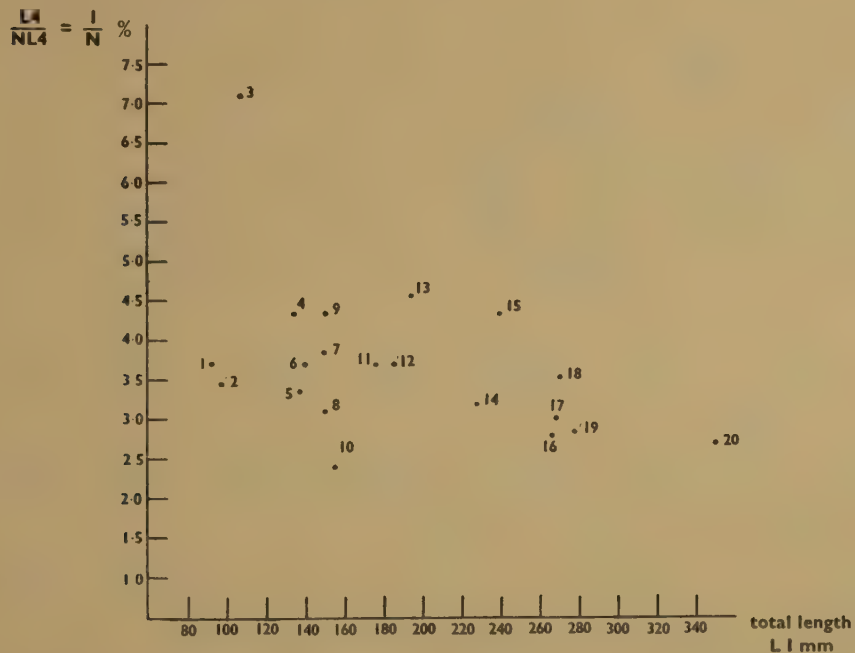


Fig. 8. Mean caudal cartilage length expressed as fraction of post-notochordal length plotted against total length of specimen in mm in twenty *Protopterus aethiopicus*. The numbers against the points refer to the specimen numbers in Table 1. $r=0.63$.

Relatively long or short cartilages may occur at any point in a tail. No. 18, for example, had twenty-eight caudal cartilages which ranged from 3.75 to 0.9 mm in length. The longest cartilage was the eighth from the posterior end of the notochord.

The mean lengths of caudal cartilages L4/N from different individuals vary greatly. This is shown in Text-figs. 7 and 8. In Text-fig. 7, the mean cartilage length expressed as a fraction of the total length of the fish L1, is plotted against the total length L1 in mm. In Text-fig. 8, mean cartilage length, expressed as a fraction of the length of the post-notochordal region L4, is plotted against L1. There is no correlation between mean cartilage length and total length and no correlation between mean cartilage length and post-notochordal length.

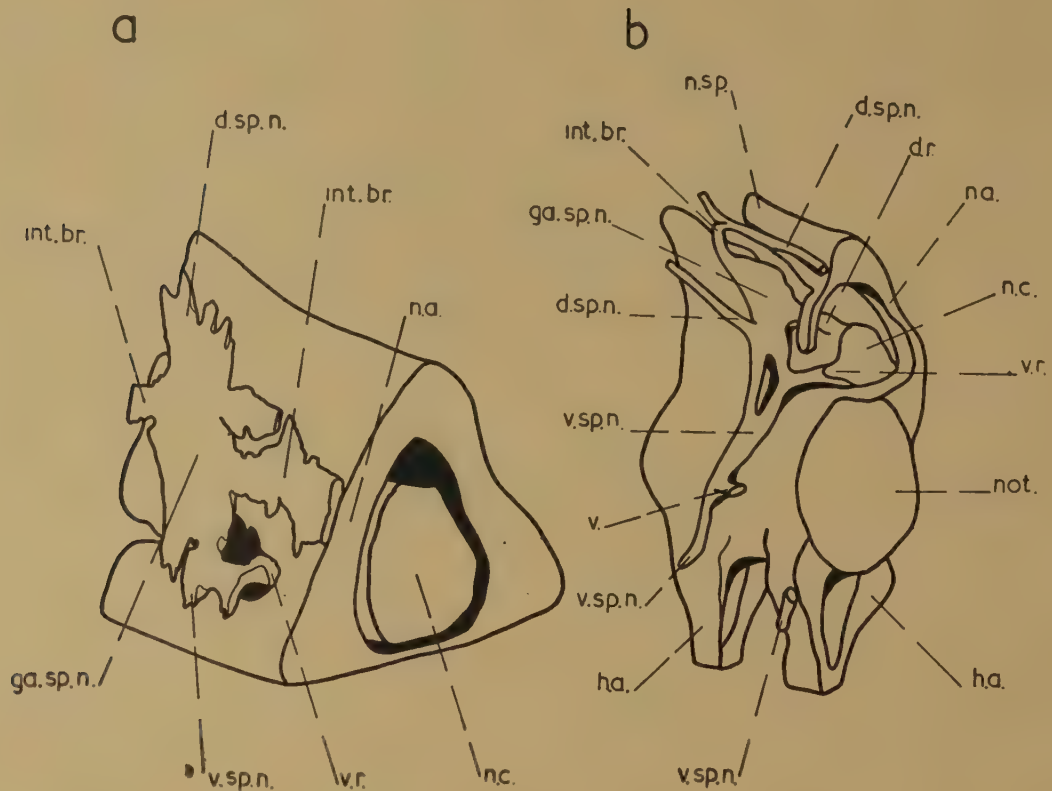


Fig. 9. Nervous system in the tail of *Protopterus*. Wax model reconstructions from serial sections. a. 303 mm *P. aethiopicus*, a post-notochordal spinal ganglion. b. 71 mm *P. amphibius*, the notochordal region just posterior to the vent.

d.r. dorsal root; d.sp.n. dorsal ramus of spinal nerve; ga.sp.n. ganglion of spinal nerve; h.a. haemal arch; int.br. dorsal and posterior intersegmental branches; n.a. neural arch; n.c. nerve cord; not. notochord; n.sp. neural spine; v. lateral line branch of vagus; v.r. ventral root; v.sp.n. ventral ramus of spinal nerve.

There is great variability in the post-notochordal region and no clear pattern emerges.

Like the skeleton, the arrangement of the nervous system is quite regular in the anterior notochordal part of the tail (Text-fig. 9b). The segmental ganglia alternate with the neural arches which are intersegmental. There are two main trunks or rami to each spinal nerve. The dorsal ramus ascends the neural arch and spine behind its ganglion and the ventral ramus passes down the corresponding

haemal arch and spine. Both rami then run beside the basal and radial elements of the skeleton and are accompanied by blood-vessels. Each ganglion gives off a dorsal intersegmental branch which accompanies the dorsal ramus of the preceding segment.

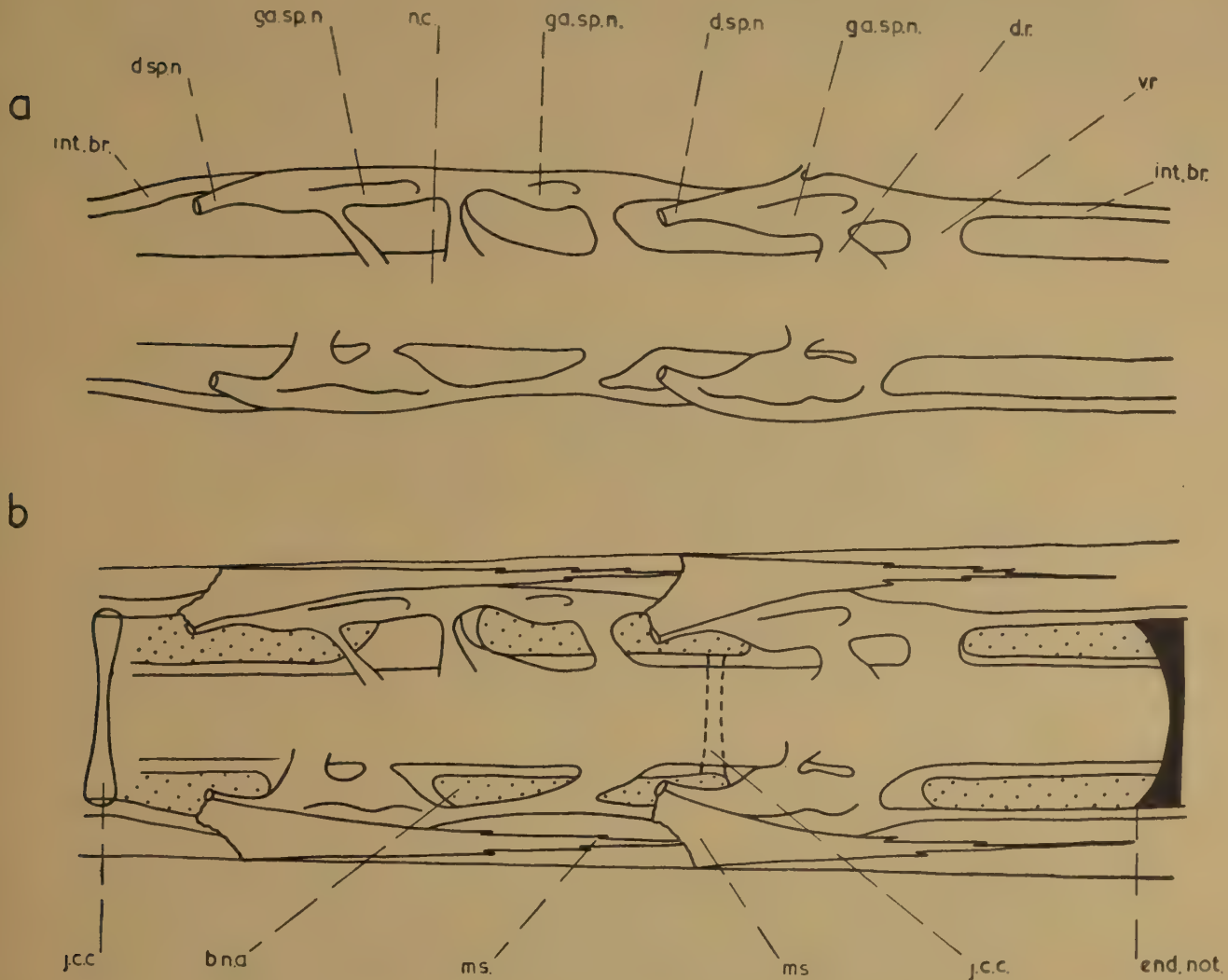


Fig. 10. *Protopterus aethiopicus*, 105 mm. Nervous system in the post-notochordal region showing irregularities in the arrangement of spinal ganglia and nerve roots. On one side there are three spinal ganglia, two of which are imperfectly differentiated from one another. On the other side there are two spinal ganglia between which there is a ventral root which accompanies the posterior intersegmental branch of spinal nerve. a., the nervous system alone. b., the nervous system in relation to the neural arches and myosepta. Cartilage dotted, end of notochord black. Reconstructed from serial sections, dorsal view. b.n.a. base of neural arch; d.r. dorsal root; d.sp.n. dorsal ramus of spinal nerve; end.not. end of notochord; ga.sp.n. ganglion of spinal nerve; int.br. posterior intersegmental branch of spinal nerve; j.c.c. joint between caudal cartilages; ms. myoseptum; n.c. nerve cord; v.r. ventral root.

In the anterior post-notochordal region and in the region of the notochord near its posterior end, there is a distortion of this arrangement. A posterior intersegmental branch takes a horizontal course to the next posterior ganglion where it is joined by fibres from this ganglion. It then ascends a neural spine as a dorsal ramus. This intersegmental branch (Plate 1, fig. 4) is the distorted proximal part of a dorsal ramus, but owing to its position it is sometimes accompanied by the ventral nerve-root of the next posterior segment (Text-fig. 10). This gives the appearance of great confusion when viewed as a series of sections. Text-figs. 11

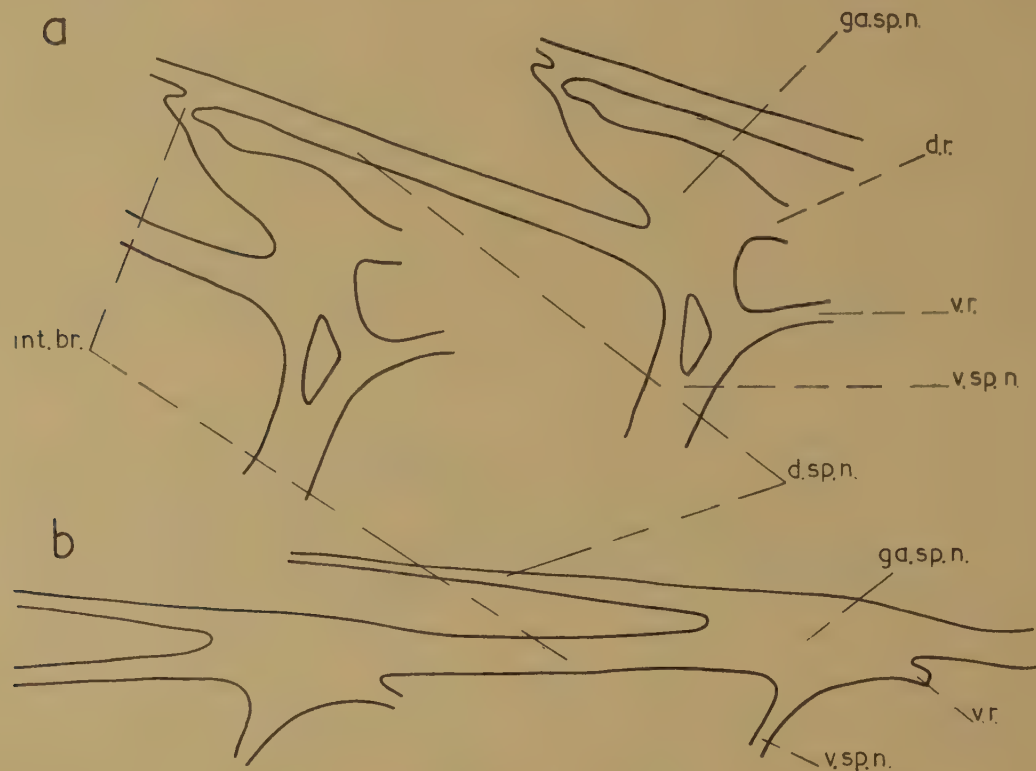


Fig. 11. Side views of the nervous system in the tail of *Protopterus*. a. typical arrangement in the anterior part of the tail; b. the distorted arrangement in the post-notochordal region; In b. the dorsal roots are situated behind the ganglia and they are not shown.

d.r. dorsal root; d.sp.n. dorsal rami of spinal nerves (in b. from preceding segment); ga.sp.n. ganglion of spinal nerve; int.br. dorsal and posterior intersegmental branches; v.r. ventral root; v.sp.n. ventral ramus of spinal nerve.

and 12 show how the nervous system is distorted in the post-notochordal region. In the posterior post-notochordal region spinal ganglia are absent and segmental spinal nerves are not developed.

There are many irregularities in the nervous system of the post-notochordal region. Successive ganglia may be incompletely differentiated from one another and may be irregular in shape. A ganglion may be present on one side of the nerve cord and a corresponding ganglion on the other be absent (Text-fig. 10). Amorphous groups of ganglion cells may occur beside the nerve cord and within

the neural arches (Plate 1, fig. 5). Sometimes a ganglion does not develop a dorsal root at all (Text-fig. 9a), and there are always great irregularities in the number of dorsal and ventral nerve roots.

The dorsal and ventral rami of the spinal nerves may have extra branches corresponding with and running parallel to the irregularly arranged basals and radials, and there are certain branches of the dorsal and ventral rami which, transgressing their own segments, run back parallel to the long axis of the tail (Text-fig. 12).

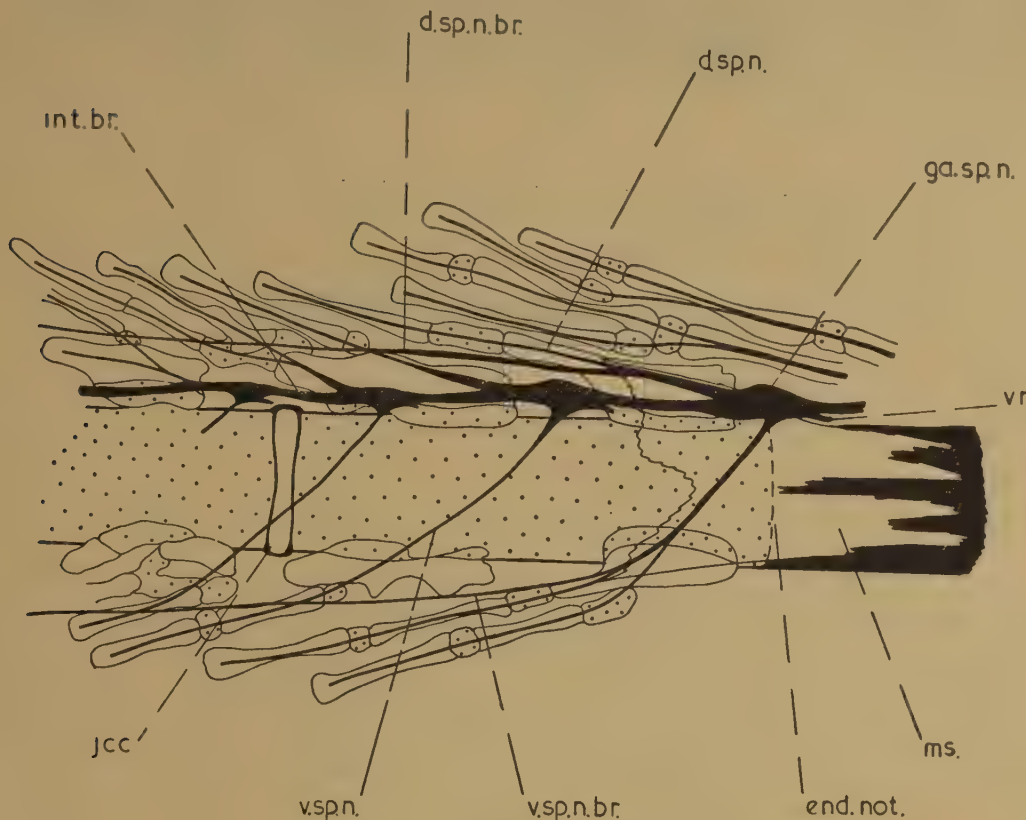


Fig. 12. Nervous system in relation to the skeleton in the post-notochordal region of *Protopterus*, based on several specimens. The boundaries between consecutive neural arches are indistinct. Cartilage dotted, bone unshaded, notochord black. Dorsal roots are not shown.

d.sp.n.br. branch from dorsal ramus of spinal nerve; v.sp.n. ventral ramus of spinal nerve; v.sp.n.br. branch from ventral ramus of spinal nerve. (For other lettering see Text-fig. 10.)

Myosepta can be seen quite well in stained and cleared preparations of the trunk region and they are arranged as in other fishes. In the tail, myosepta become so distorted during growth and differentiation that similar preparations fail to show their dispositions (Text-fig. 13).

As in the notochordal tail, the central regions of the neural and haemal arches are intersegmental and the neural and haemal spines lie in the myosepta; but at the level of the caudal cartilages, the myosepta are extended antero-posteriorly

as overlapping sheaths of connective tissue. They do not divide the tail into segments by discrete transverse partitions and the anterior part of each segment lacks a horizontal septum.

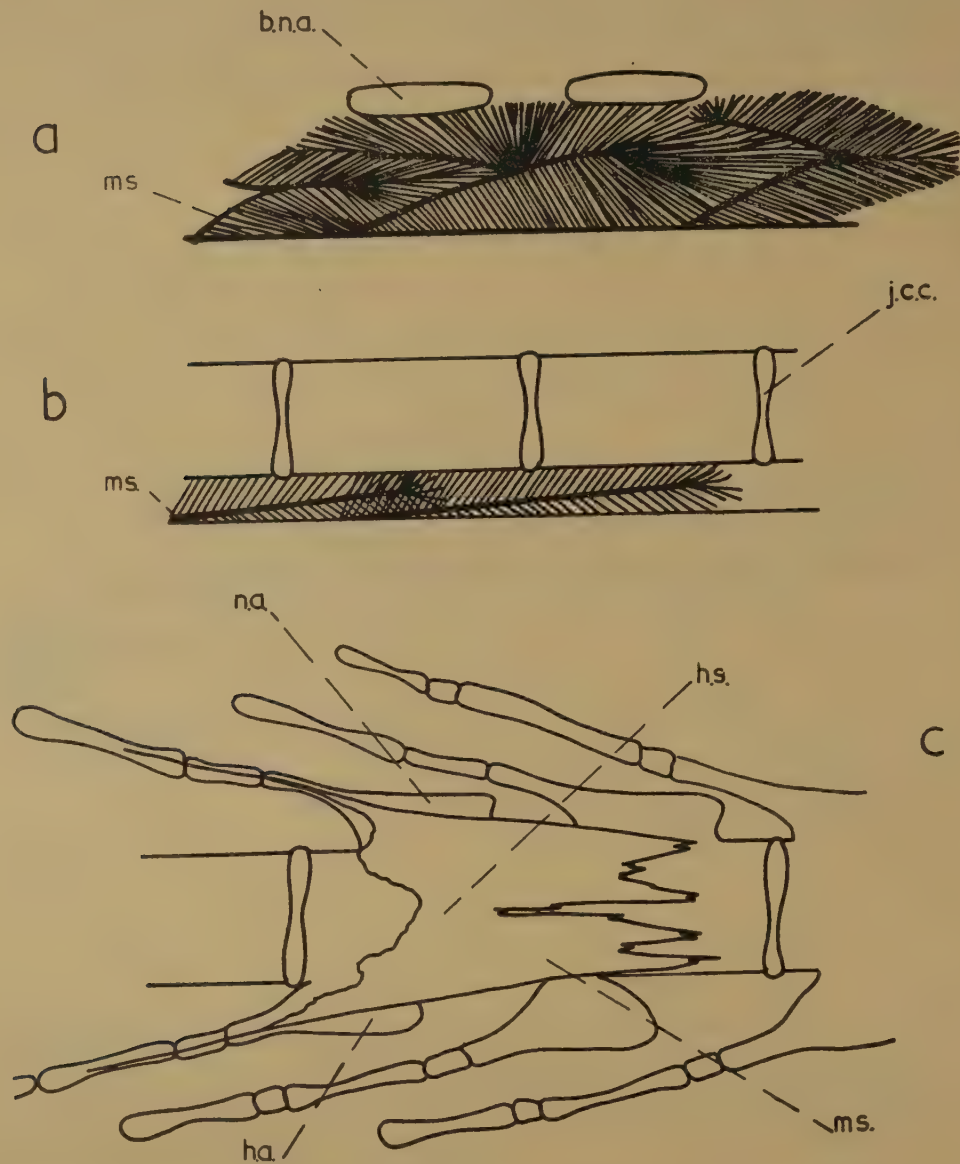


Fig. 13. Arrangement of myosepta in the post-notochordal region of *Protopterus*. a. Horizontal section at level of bases of neural arches. b. Horizontal section at level of caudal cartilages but dorsal to horizontal septum. c. Side view; for clarity only one myoseptum is shown. b.n.a. base of neural arch; h.a. haemal arch; h.s. horizontal septum; j.c.c. joint between caudal cartilages; ms. myoseptum; n.a. neural arch.

There are many irregularities in the arrangement of the myosepta. These correspond to the irregularities in the arrangement and structure of the arches and segmental ganglia. Where the arches are composite or double structures or

where there are two distinct arches on a single caudal cartilage, two myosepta may be present. Since there may be these double segments where differentiation into two is incomplete and since, in the posterior post-notochordal region, only partially differentiated segments may be present, it is impossible to state the precise number of segments present in an individual.

Text-fig. 13 and the developmental stages already described, show however, that each joint between the caudal cartilages represents a region where a segment is differentiating, even though it may be incomplete. Table 2 has been compiled by taking the number of joints between the caudal cartilages as representing the minimum number of post-notochordal segments. The number of post-occipital notochordal segments was determined by counting the neural arches and then adding one, because there are two post-occipital myotomes in front of the first neural arch (Agar 1906).

TABLE 2. NUMBER OF SEGMENTS IN SIX *Protopterus aethiopicus*

The column on the left refers to the specimen number in Table 1.

No.	Post-occipital notochordal	Minimum number post-notochordal	Minimum total number
13	74	21	95
9	81	22	103
11	78	26	104
12	79	26	105
8	74	31	105
20	74	36	110

There is great variability in the number of segments present. Agar (1907) stated that the number of post-occipital myotomes in *Lepidosiren* was about 110 and in *Protopterus annectens* about 65, but he was dealing with young specimens and he does not mention the post-notochordal region.

YOUNG *AMBLYSTOMA* AND *TRITURUS*

A post-notochordal tail is not developed at all in many *Amblystoma* specimens but if developed, it appears when the larva is between 30 and 50 mm in length. At first the growing tip of the nerve cord extends further back than the end of the notochord. As this process continues, a rod of post-notochordal cartilage, at first jointless, is formed beneath the nerve cord.

In a 106 mm specimen there is a rod 8 mm in length composed of six caudal cartilages behind the notochord. These are separated from one another by poorly formed joints, regions where the density of cartilage cells to matrix is high, and around which there is a ring of cells which partially invade the joint. Each caudal cartilage is sheathed by a smooth-surfaced cylinder of bone. The posterior cylinders tend to be less constricted at the waist than the notochordal centra further forwards.

Each cylinder bears neural and haemal arches. The arches on the posterior cylinder are in an earlier stage of development than those on the others. Here they consist of unossified pieces of cartilage which barely meet above the nerve

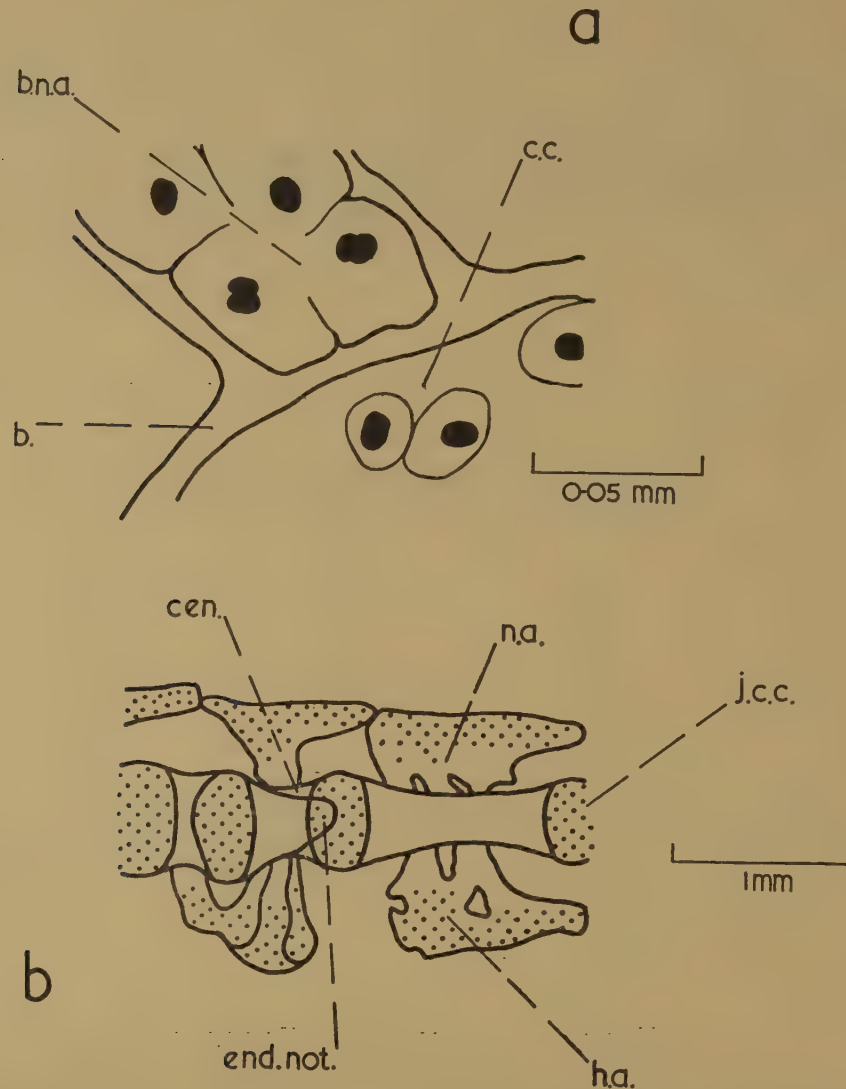


Fig. 14. *Amblystoma tigrinum*, 106 mm. a. Transverse section showing base of post-notochordal neural arch. b. Skeleton of tail at junction of notochordal and post-notochordal regions, from a dissection. In b. cartilage dotted, bone unshaded.
b. bone; b.n.a. base of neural arch; c.c. caudal cartilage; cen. centrum of last notochordal vertebra; end. not. end of notochord; h.a. haemal arch; j.c.c. joint between caudal cartilages; n.a. neural arch.

cord and beneath the caudal blood-vessels, and there are no neural and haemal spines. The anterior arches form a more complete covering of cartilage around the nerve cord and caudal blood-vessels, and there are neural spines of cartilage, disposed horizontally so that each extends back to touch the dorsal anterior face

of the next posterior arch. The neural arches are ossified around their bases (Text-fig. 14a) and there is a little additional membrane bone which extends them anteriorly and posteriorly. The cartilage of the arches is separated from the caudal cartilage by the bony cylinders. The cylinders are rather longer than the centra of the notochordal region and consequently these arches tend to be wider antero-posteriorly than those above the notochordal centra.

The end of the notochord is situated in the joint between the anterior caudal cartilage and the last notochordal centrum (Text-fig. 14b). The elastica externa is fully intact and extends around the posterior end of the notochord. It therefore separates the vacuolated tissue of the notochord from the cartilage of the joint. The haemal arch of the last notochordal centrum is abnormal and is partly shared by the next anterior centrum. This is vestigial and lacks a neural arch.

There are traces of muscles as far back as the posterior caudal cartilage but spinal ganglia cannot be distinguished.

In a 125 mm specimen there is a post-notochordal rod 9 mm in length. Joints divide it into five caudal cartilages similar to those described above. There are traces of additional cartilages, joints and bony cylinders forming posteriorly and four well developed post-notochordal neural and haemal arches. Spinal ganglia are incompletely differentiated, but small groups of ganglion cells are present on either side between the post-notochordal neural arches. There are no distinct myosepta and muscles are vestigial.

The elastica externa at the end of the notochord has broken down (Plate 2, fig. 17) and is embedded in the anterior caudal cartilage within the ossified cylinder. The vacuolated tissue of the notochord does not extend beyond the last normal centrum.

A post-notochordal tail was found in larvae of all three British species of *Triturus* but as in *Amblystoma* it is not developed in all specimens. Among fifty young newts (*T. vulgaris*) taken from a pond in July, ranging from 19 to 28 mm in length, post-notochordal cartilage was present in thirty but in some it was very poorly developed. In ten it was well developed, and in one of these it was exceptional, being over four times the length of the next longest rod, when the lengths are expressed as percentages of the total lengths of the specimens (See Table 3).

TABLE 3. CLEARED PREPARATIONS OF TEN YOUNG *Triturus* STAINED IN BORAX CARMINE

Length of post-notochordal rod as a percentage of total length	Total length mm.
20.0	19
4.9	23
4.75	21
4.75	20
3.5	24
3.4	28
3.2	26
2.5	28
2.4	25
2.3	26

The early stages in the development of the post-notochordal rod are like those described in *Amblystoma*. The smallest *Triturus* in which the rod was beginning to form measured 13 mm. In its early stages, the anterior end of the rod is quite

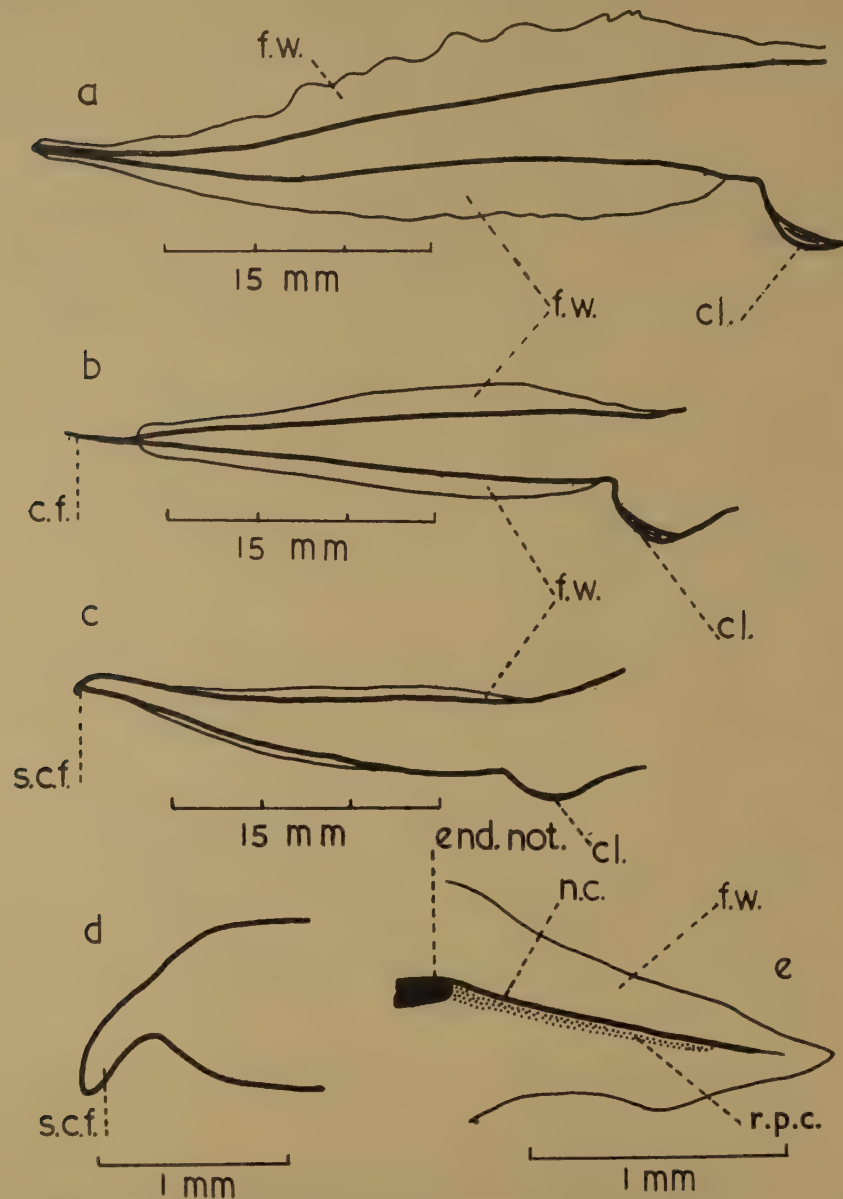


Fig. 15. Tails of *Triturus*. a. 83 mm breeding male *T. vulgaris*. Post-notochordal region about 10 mm. b. 62 mm breeding male *T. helveticus*. Post-notochordal region about 8 mm. c. 58 mm male *T. helveticus* with degenerating caudal filament and reduced median fin-webs. d. Tip of tail in c. more highly magnified. e. 23 mm *Triturus* sp., post notochordal region. c.f. caudal filament; cl. cloaca; end.not. end of notochord; f.w. median fin-webs; n.c. nerve cord; r.p.c. rod of post-notochordal cartilage; s.c.f. stump of caudal filament.

distinct from the posterior end of the notochord, being separated from it by the elastica externa (Plate 2, fig. 15). This then breaks down and disappears. The rod of cartilage may form a straight extension to the notochord (Plate 3, fig. 35)

or it may be set at an angle dorsally or ventrally to the long axis of the notochord (Text-fig. 15e).

Normally the cartilaginous rod remains unjointed and post-notochordal ganglia do not develop in the larva; but during a prolonged search, further differentiation in the post-notochordal region was found in two specimens. These tails may have regenerated.

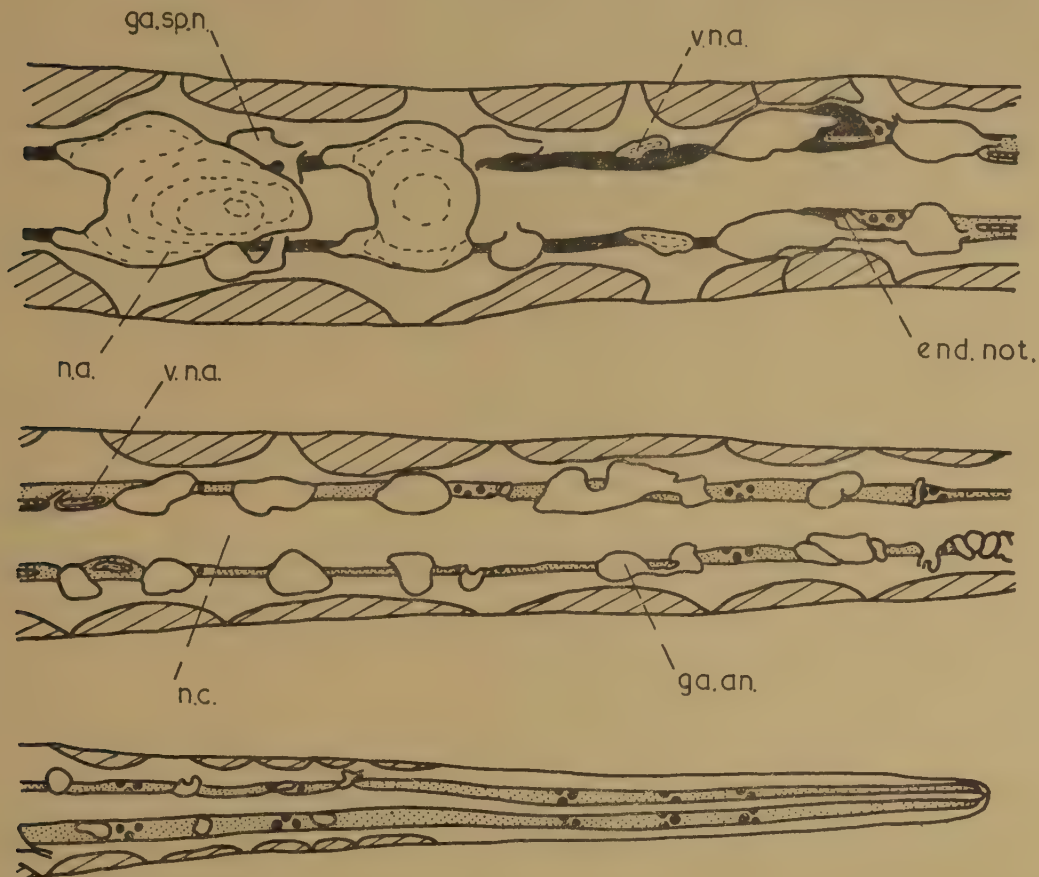


Fig. 16. Part of the tail of a 19 mm *Triturus helveticus*. Length of post-notochordal region 3.5 mm. Reconstructed from serial sections, dorsal view. Post-notochordal caudal cartilages, small dots; joints between caudal cartilages, large dots; notochord black; segmental muscles shaded.
end.not. end of notochord; ga.an. anlage of segmental ganglion; ga.sp.n. ganglion of spinal nerve; n.c. nerve cord; v.n.a. vestigial neural arch.

A ten-jointed post-notochordal rod is shown in Text-fig. 16. The first joint lies at the anterior end of the first caudal cartilage. A joint is shown in Plate 2, fig. 11. The joints are similar to those in *Amblystoma*.

There are traces of neural arches in the form of minute plates of bone on the first caudal cartilage. They do not meet dorsally around the nerve cord. There are very slight traces of bone around the anterior caudal cartilages but a distinct

cylinder of bone is absent. The nerve cord runs the whole length of the post-notochordal tail and on each side there are the anlagen of spinal ganglia. A number of myomeres have differentiated on either side of the caudal cartilages. Segmentation is very confused and some of the ganglionic anlagen are incompletely differentiated from one another.

The post-notochordal tail has only a transitory existence in the larva (Table 4). Its gradual disappearance (Plate 3, figs. 24 to 29) occurs at or just before metamorphosis, and was observed many times.

TABLE 4. CONDITION OF THE TAIL TIP IN THIRTY YOUNG *Triturus* DETERMINED BY SECTIONING
L1, total length of specimen. Post-notochordal cartilage:— 0, absent. X, present as trace. +, well developed. —, degenerating.

L1 mm.	<i>T. vulgaris</i> and <i>T. helveticus</i>	<i>T. cristatus</i>
4	0	
11	0	
13		X
14	X 0	
15	X++	
16	0	
19	+ 0	
22	+ +	0
23	X X	
24	X	
27	+ —	
28	+	
29	0 0	
30	—	
31	—	
34	—	
35		+
36		+ 0
37	—	
38		+

Dorsal and ventral median fin-webs are continued into the post-notochordal region and join posteriorly to form a pointed tip to the tail. A caudal artery and vein are present (Plate 2, fig. 12) and there is a variable arrangement of smaller blood-vessels in the fin-webs (Plate 3, fig. 33) which can be seen in living specimens.

When the post-notochordal region is degenerating, these blood-vessels become blocked by blood-corpuscles, simultaneously, the median fin-webs decrease in width, and pigment accumulates both at their regressing edges and at the extreme tip of the tail. As the blood supply fails and the tissues become increasingly necrotic the larva swims about with a mass of dead cells at the tail tip. Ultimately the mass is sloughed off and the process begins again. The post-notochordal rod itself undergoes histolysis (Plate 2, fig. 19) and dark granules are present in its remnants. The cartilaginous matrix eventually disappears altogether, and the degenerative process proceeds, and may even affect the extreme end of the notochord.

ADULT *TRITURUS*

After metamorphosis, there is normally no post-notochordal tail in young terrestrial newts but it is present in adult males and females of all three British species. It is least developed in *T. cristatus* and most developed in *T. helveticus* where it reaches its maximum in breeding males (Text-fig. 15). In *T. vulgaris* dorsal and ventral median fin-webs are continued to the tip of the tail, but in the male *T. helveticus*, unlike the other two species, the fin webs are continued only on to the anterior part of the post-notochordal tail, which posteriorly forms a caudal filament. Measurements from living specimens show that the filament grows out beyond the fin webs and is not formed by their degeneration. The internal structure of the post-notochordal tail is similar in all three species. A fully developed post-notochordal tail in a 68 mm breeding male *T. helveticus* is described below.

Anteriorly in the post-notochordal region there are four opisthocoelous cartilages (Plate 2, fig. 14), separated by joints which are less well developed than in the notochordal region. Each cartilage is surrounded by a rough-surfaced cylinder of bone and bears bony neural and haemal arches with spines. The cartilages are intersegmental and occupy similar positions to the vertebral centra further forward. A caudal artery and vein, segmental muscles and four pairs of segmental spinal ganglia are present; and the structure and arrangement are similar to that in the notochordal region. A rod of cartilage and the nerve cord continue in the filament which is darkly pigmented and projects 7 mm beyond the fin-webs (Plate 2, fig. 16).

There are many irregularities in the post-notochordal region of adult newts. The number of cartilages varies. They may be relatively long and narrow or broad and short, and may be amphicoelous (Plate 2, fig. 18). The arches may be vestigial or cartilaginous and spinal ganglia may be absent. The musculature may be vestigial and about ten of the neural arches at the end of the tail lack zygapophyses (Plate 3, fig. 34).

It is sometimes difficult to determine the anterior boundary of the post-notochordal region for two reasons.

Intra-vertebral cartilage which may occur in the notochordal region (see Mookerjee 1930) forms in the vertebral centra where the vacuolated tissue of the notochord previously existed. As growth proceeds, the notochordal sheath disappears, and the intra-vertebral cartilage may join up with the inter-vertebral cartilage of the joints to look like post-notochordal cartilage.

More often in the centra, the notochord is replaced by marrow cavities (Plate 2, fig. 13) and similar cavities may be formed in the post-notochordal region.

In the males of *T. helveticus* and to a limited extent in females, considerable changes in the shape of the tail vertebrae take place when the post-notochordal tail reaches its maximum. See Plate 3, figs. 30 and 32. The neural and haemal spines become shortened antero-posteriorly by resorption of bone on their anterior faces, and they become lengthened dorsoventrally by additional bone.

In both sexes the post-notochordal tail becomes much reduced at the end of the breeding season and the posterior rod of cartilage and caudal filament if present (Text-fig. 15c and d) disappear. Sections of the degenerating tail tip show many

dead cells and granules in the cartilaginous rod and masses of dark pigment in the tissues around the cartilage. The cartilage is destroyed by invading cells and gradually disappears. These cells first appear outside the cartilage and seem to have a two-fold action. On the one hand they probably exude secretions which dissolve the matrix of the cartilage from which activity only granules remain. On the other hand by amoeboid movement, they ingest the granules together with the actual cartilage cells. (See Plate 2, figs. 21 to 23).

During degeneration of the post-notochordal tail, the fin-webs of the entire tail are gradually resorbed and disappear, and neural and haemal spines undergo changes which are the reverse of those described above (Plate 3, fig. 31).

DISCUSSION

A post-notochordal tail develops in Dipnoi and Urodela when the nerve cord outgrows the notochord posteriorly or outgrows the notochordal vertebrae in adult newts. It does not occur in the absence of the nerve cord.

H. Holtzer (1952), using the techniques of experimental embryology, studied the formation of cartilage in the trunk region of Urodela. In the absence of the notochord, a massive cartilaginous rod was formed lying ventral to the nerve cord in the position normally occupied by the notochord. If the nerve cord was rotated 180 degrees around its long axis, the rod formed dorsally. This suggested that the biochemical make-up of the ventral half of the nerve cord in urodeles differs from that of the dorsal half and that the precartilaginous rod cells responded to biochemical influences in the ventral part of the nerve cord.

The notochord does not regenerate in urodele tails but a post-notochordal cartilaginous rod is induced from the tail blastema by the regenerating nerve cord (S. Holtzer 1956). It may be inferred that a similar mechanism is at work in the spontaneous formation of post-notochordal tails, both in Dipnoi and Urodela.

Why the growth of the notochord should fail to keep pace with the growth and differentiation of the other tissues in the end of the tail is unknown but both Dipnoi and Urodela appear to possess the same genetic mechanism endowing them with this potentiality.

It is probable that post-notochordal tails occur spontaneously in every genus of urodele. Post-notochordal cartilage was found in a *Necturus* (Plate 2, fig. 20) and in two *Salamandra maculosa* 28 and 40 mm in length. However development was not observed in these specimens, and regeneration could have taken place.

Rana temporaria, *Xenopus laevis* and *Bufo bufo* tadpoles, and a few embryo to adult stages of the caecilian *Hypogeophis rostratus* were examined but no post-notochordal cartilage was present. Despite an extensive search; however, it is still possible that a post-notochordal tail may occasionally occur in Anura.

In the early fossil amphibian *Ichthyostega* the posterior part of the tail is supported by a bony rod which tapers distally and continues almost to the tip of the tail (Jarvik, 1952). This rod, the so-called urostyle, seems to represent modified vertebral elements and it is pierced anteriorly by a narrow longitudinal canal. This may have contained the notochord but it is possible that, in part at any rate,

the urostyle was a post-notochordal rod like that in Dipnoi and Urodela. If the dipnoan-urodele type of post-notochordal tail does not occur in fishes apart from Dipnoi and other crossopterygians, then it is possible that lower tetrapods inherited this arrangement from their crossopterygian ancestors.

Protopterus circulates water in its nest by movements of the tail (Greenwood 1958) but the precise function of the post-notochordal region is obscure. Moreover in dipnoan evolution (see Westoll 1949), the tail ceased to be heterocercal and thus its terminal portion became of less importance in locomotion. On the tail of *Protopterus* there is a bend or break in the main lateral line (see Graham-Smith 1936) and posteriorly the line continues at a lower level. The position of the end of the notochord relative to the break is variable. It is usually well behind the break but part of the lateral line which continues at the lower level is borne by the post-notochordal region. Other neuromasts are also present.

In male *Triturus*, the tail is bent round and the post-notochordal region is waved in front of the female during courtship. Nevertheless in nearly all animals the post-notochordal region appears to have no special function.

However, though it is probable that most morphological characters are adaptive, an aberration in a developmental process that conferred no disadvantage may in this particular case have been retained to become widespread in Dipnoi and Urodela.

ACKNOWLEDGMENTS

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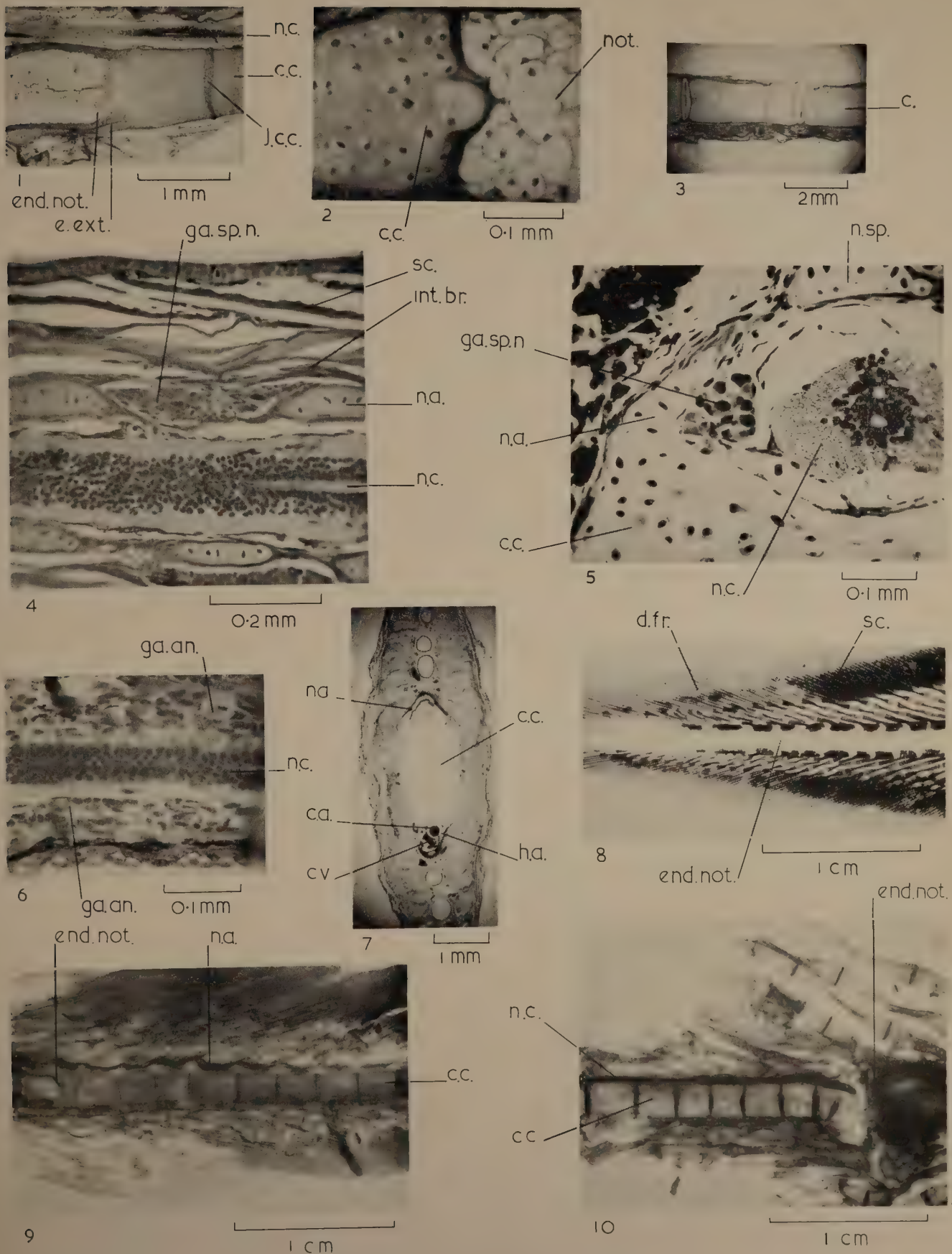
PLATE 1

PLATE 1

Protopterus. Figs. 1-2, 5-6, 10, *P. amphibius*. Figs. 3-4, 7-9, *P. aethiopicus*.

- Fig. 1. Length 111 mm. Median sagittal section showing attachment of first caudal cartilage to end of notochord. The notochordal sheath is absent at the extreme end of the notochord. Iron haematoxylin-eosin.
- Fig. 2. Length 71 mm. Horizontal section showing attachment of first caudal cartilage to end of notochord. The anterior face of the first caudal cartilage is expanding into the vacuolated tissue of the notochord. Iron haematoxylin-ponceau S.
- Fig. 3. Length 380 mm. Horizontal section through caudal cartilages showing cavities in caudal cartilages and pads of tissue between joints. Masson's trichrome.
- Fig. 4. Length 105 mm. Horizontal section dorsal to caudal cartilages showing posterior intersegmental branch of spinal nerve and next posterior ganglion. Iron haematoxylin-ponceau S.
- Fig. 5. Length 111 mm. Transverse section showing spinal ganglion cells inside neural arch. Iron haematoxylin-eosin.
- Fig. 6. Length 42 mm. Horizontal section showing anlagen of spinal ganglia dorsal to caudal cartilage. Azocarmine-Mallory.
- Fig. 7. Length 303 mm. Transverse section of post-notochordal tail. Iron haematoxylin-ponceau S.
- Fig. 8. Length 185 mm. Part of tail. Many of the scales have been removed in order to show internal skeleton. Alizarin cleared in glycerine.
- Fig. 9. Length 350 mm. Dissection of post-notochordal tail. Methyl green cleared in oil of wintergreen.
- Fig. 10. Length 401 mm. Dissection of post-notochordal tail. Mayer's haemalum cleared in oil of wintergreen.

c. cavity in caudal cartilage; c.a. caudal artery (dorsal aorta); c.c. caudal cartilage; c.v. caudal vein; d.fr. dermal fin-ray; e.ext. elastica externa; end.not. end of notochord; ga.an. anlage of spinal ganglion; ga.sp.n. ganglion of spinal nerve or ganglion cells; h.a. haemal arch; int.br. posterior intersegmental branch of spinal nerve; j.c.c. joint between caudal cartilages; n.a. neural arch; n.c. nerve cord; not. notochord; n.sp. neural spine; sc. scale (s).



The post-notochordal tail in Dipnoi and Urodela.

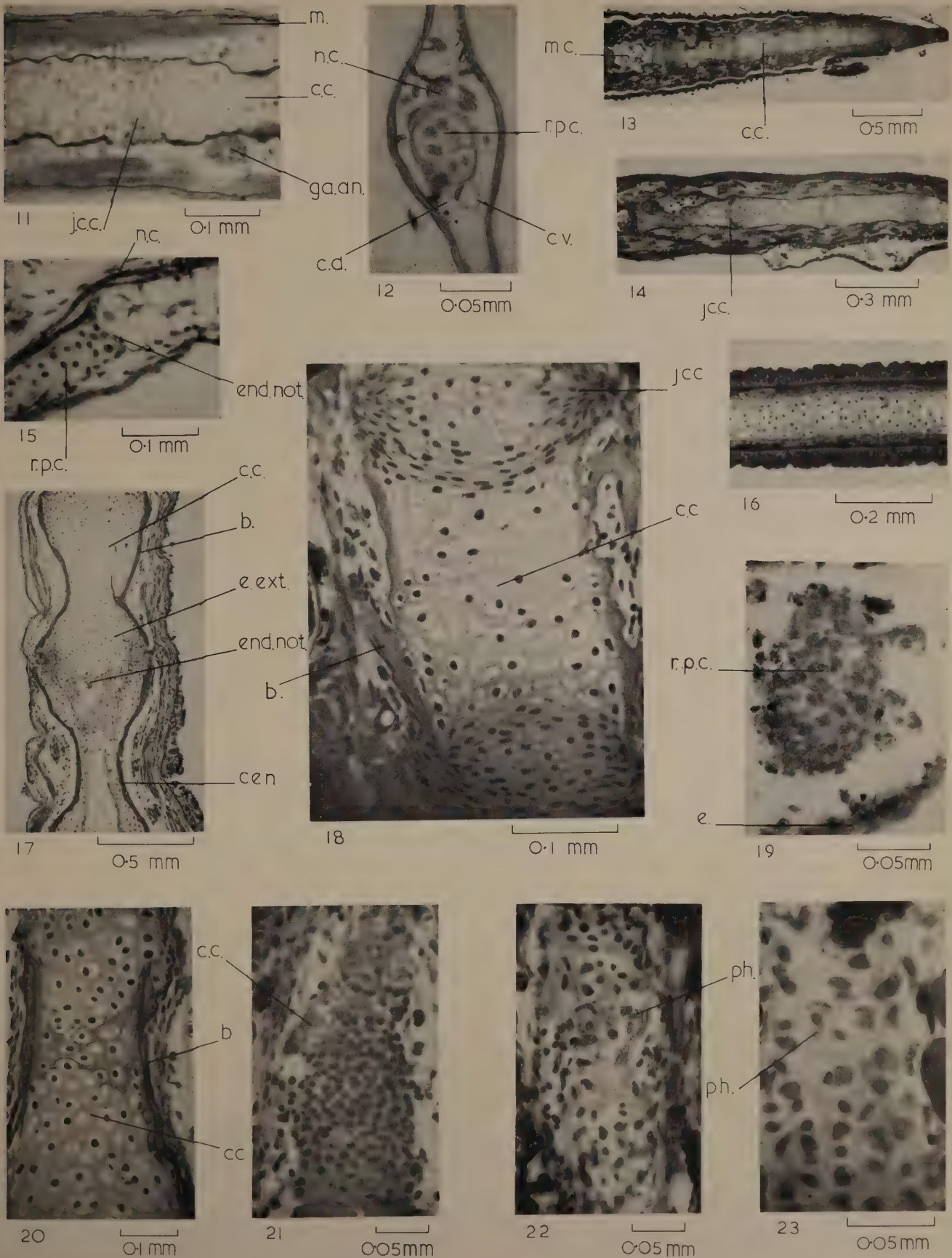
PLATE 2

PLATE 2

Amblystoma, *Triturus* and *Necturus*. Fig. 17, *A. tigrinum*. Figs. 11, 12, 14–16, *T. helveticus*.
Figs. 13, 18, 21–23, *T. vulgaris*. Fig. 19, *Triturus* sp. Fig. 20, *N. maculosus*.

- Fig. 11. Length 19 mm. Horizontal section through post-notochordal tail. Azocarmine-Mallory.
- Fig. 12. Length 23 mm. Transverse section through post-notochordal tail. Azocarmine-Mallory.
- Fig. 13. Length 96 mm. Adult female. Horizontal section through end of tail. Iron haematoxylin-ponceau S.
- Fig. 14. Length 68 mm. Adult male in breeding condition, showing joints between caudal cartilages. Azocarmine-Mallory.
- Fig. 15. Length 15 mm. Median sagittal section showing attachment of post-notochordal cartilaginous rod to end of notochord. Iron haematoxylin.
- Fig. 16. Horizontal section posterior to that shown in Fig. 14, through caudal filament showing central rod of cartilage. Azocarmine-Mallory.
- Fig. 17. Length 125 mm. Horizontal section showing end of notochord. Mayer's haemalum-eosin.
- Fig. 18. Length 82 mm. Horizontal section showing ossification of caudal cartilage and tendency for cartilage to be amphicoelous. Azocarmine-Mallory.
- Fig. 19. Length 31 mm. Transverse section showing histolysis of post-notochordal cartilaginous rod. Azocarmine-Mallory.
- Fig. 20. Length 241 mm. Horizontal section showing ossification of caudal cartilage. Iron haematoxylin-ponceau S.
- Fig. 21. Length 82 mm. Horizontal section showing histolysis of caudal cartilage in male after breeding. Azocarmine-Mallory.
- Figs. 22–23. Length 82 mm. Horizontal section from another male after breeding showing cells in caudal cartilage which are probably phagocytic. Azocarmine-Mallory.

b. bone; c.a. caudal artery (dorsal aorta); c.c. caudal cartilage; cen. centrum of vertebra; c.v. caudal vein; e. epidermis; e.ext. elastica externa; end.not. end of notochord; ga.an. anlage of spinal ganglion; j.c.c. joint between caudal cartilages; m. muscle; m.c. marrow cavity of vertebra; n.c. nerve cord; ph. cells which are probably phagocytic; r.p.c. rod of post-notochordal cartilage.



The post-notochordal tail in Dipnoi and Urodela.

PLATE 3

PLATE 3

Triturus. Figs. 24-34, *T. helveticus*. Fig. 35, *Triturus* sp.

Figs. 24-29. Length from 26 to 25 mm. Necrosis of tail tip of young living newt kept in aquarium. Fig. 24, Jan. 20th. Fig. 25, Jan. 22nd. Fig. 26, before and Fig. 27, after wriggling on Jan. 29th, showing sloughing off of dead tissue. Fig. 28, Feb. 5th. Fig. 29, Feb. 12th.

Fig. 30. Tail skeleton of aquatic adult male killed during the breeding season. Alizarin cleared in glycerine.

Fig. 31. Tail skeleton of terrestrial adult male. Alizarin cleared in glycerine.

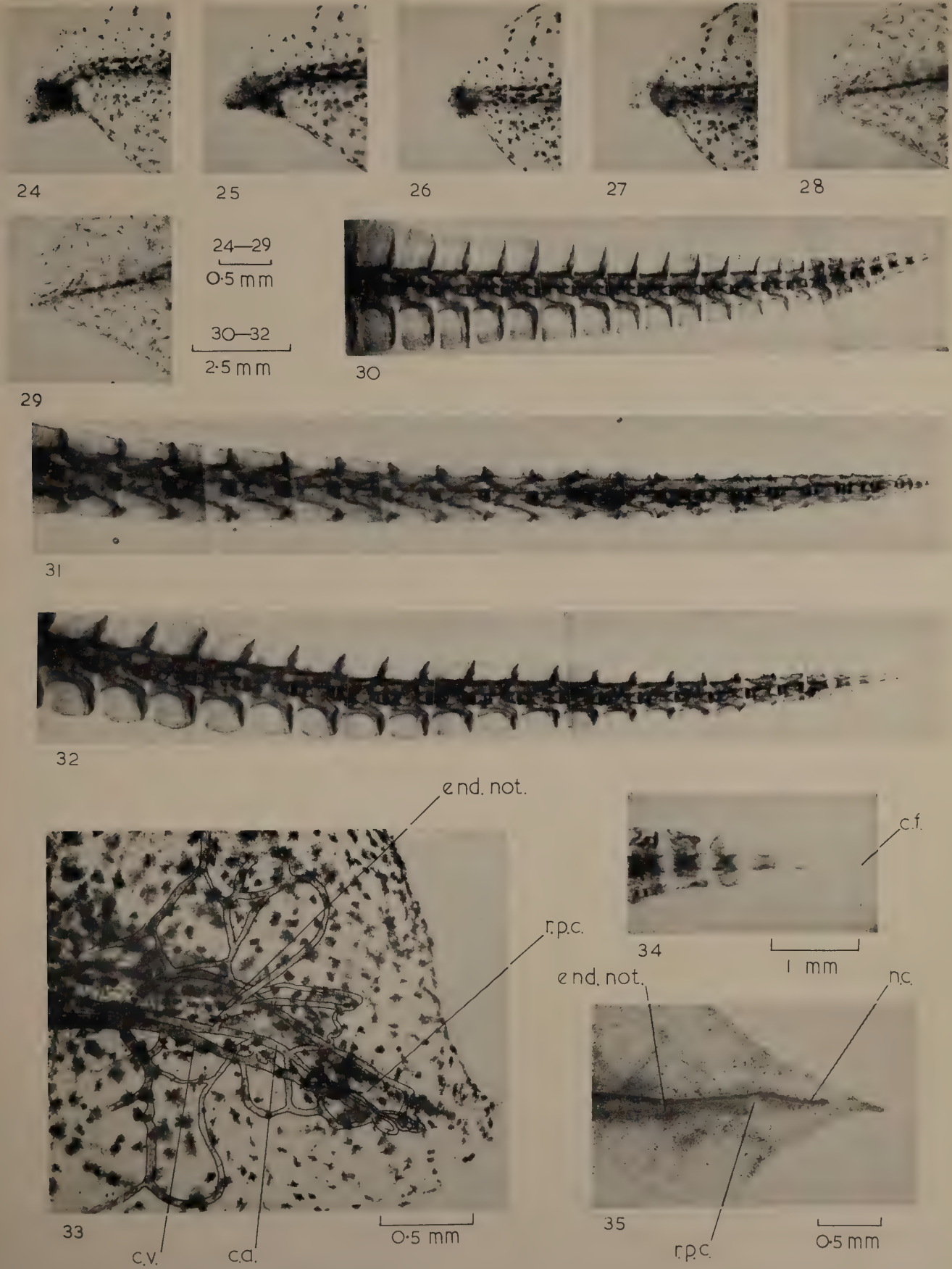
Fig. 32. Tail skeleton of aquatic adult female killed during the breeding season. Alizarin cleared in glycerine.

Fig. 33. Length 28 mm. Tip of tail of young living newt. The blood-vessels have been outlined in black.

Fig. 34. Part of Fig. 30 more highly magnified. Alizarin cleared in glycerine.

Fig. 35. Length 29 mm. Tail tip showing rod of post-notochordal cartilage. Borax carmine cleared in oil of wintergreen.

c.a. caudal artery (dorsal aorta); c.f. caudal filament; c.v. caudal vein; end.not. end of notochord;
n.c. nerve cord; r.p.c. rod of post-notochordal cartilage.



The post-notochordal tail in Dipnoi and Urodela.

A Revision of the Genus *Pygophora* Schiner (Diptera: Muscidae)

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[Accepted 12th December, 1961]

(With 124 figures in the text)

The genus *Pygophora* Schiner (Muscidae: Coenosiinae) is fully revised. The zoogeography of the genus is discussed and keys are given to the species in both sexes. Fifty-three species are included in *Pygophora*, of which seventeen are new species; seven specific names are newly synonymized and there are ten new combinations.

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INTRODUCTION

The present paper, giving a revision of the genus *Pygophora* Schiner, is the first part of a general revision of the Muscidae of the subfamily Coenosiinae occurring in the Australasian and Oriental Regions; the coenosiine fauna of the remainder of the Old World is fully treated by Emden (1940) [Ethiopian Region] and by Hennig (1960, 1961 and in press) [Palaeartic Region]. *Pygophora* is a distinctive genus and can be distinguished from other coenosiine genera occurring in the Australasian and Oriental regions by the key given in a later section. Although pre-eminently Austro-Malayan in distribution, *Pygophora* extends also into tropical Africa and Madagascar and the few species occurring in the Ethiopian Region and Malagasy Region are dealt with in this paper so as to give a full generic revision.

Pygophora was described by Schiner (1868) for a single new species (*P. apicalis* Schiner), generally related to *Coenosia* Meigen but differing in the male by the possession of a curious preapical ventral lobe on the hind tibia—a character which, it is now appreciated, is not of generic significance, although formerly used by Stein as the only means of distinguishing *Pygophora* from *Coenosia*. Stein (1900), in his first paper dealing with the present group, described a species with the lobe as *C. (Pygophora) lobata* Stein, thus at this time, though not actually saying so, regarding *Pygophora* as a subgenus of *Coenosia*. In his later papers, Stein (1904, 1906, 1909, 1910a, 1910b, 1915, 1918, 1919b, 1920a, 1920b) described numerous species, assigning those possessing the male hind tibial lobe to *Pygophora* and those otherwise similar but lacking the lobe to *Coenosia*; thus the two genera could not be distinguished in the female sex and very closely allied species were placed in different genera, depending on the presence or absence of the tibial lobe in the male. In his major paper on the anthomyiid (muscid) genera of the world Stein (1919a) retained the tibial character as the distinguishing feature of *Pygophora* and *Coenosia*, but Malloch (1921, 1922) pointed out that the male tibial lobe could not be upheld as a generic character and drew attention to other more important characters which always enable *Coenosia* and *Pygophora* to be distinguished in both sexes. It is now clear that *Coenosia* and *Pygophora* are not especially closely related, the former coming in a group of coenosiine genera in which there is only one pair of reclinate upper frontal bristles on the head, and *Pygophora* falling in the group of genera in which there are two pairs of reclinate frontal setae; thus *Pygophora* is much more nearly related to *Lispocephala* Pokorny (type-species: *L. alma* (Meigen)) than to *Coenosia* Meigen (type-species: *C. tigrina* (Fabricius)).

Stein (1915) gave a key to five species of *Pygophora* (*sensu* Stein), and Malloch (1922) published a key to the thirteen species known to him; other than these the only keys hitherto have been those of Emden (1940) to five species from Africa and the Seychelles, and a recent key by Paramonov (1961) to the Australian species.

The present revision includes fifty-three species in the genus *Pygophora*, of which seventeen are new species described in this paper. Forty-six previously described species are involved in this revision and the holotypes or syntypes of forty-one of these have been examined; in the case of four other recently described species

paratypes have been examined from the type series (undoubtedly conspecific with the holotypes); and in the case of the one remaining species the holotype is known to be lost (see under *P. hirtimana* Malloch). Lectotypes have been designated and labelled in all cases where a species was described from more than one type specimen, and the syntypes remaining after lectotype designation have been labelled as paralectotypes. From the examination of types ten names are found to be synonymous, of which seven are newly established synonyms; thus thirty-six of the forty-six previously described species are upheld. Nine species hitherto placed in *Coenosia* and one previously in *Lispocephala* are here included in *Pygophora* and there are thus ten new combinations involved in this revision. One species recently described in *Pygophora*, namely *P. comuni* Paramonov, belongs in the very closely related genus *Cephalispa* Malloch which will be revised in a forthcoming paper. The relation of *Cephalispa* with *Pygophora* and *Lispocephala* is discussed in a later section (p. 401).

There is some confusion in the literature because of the misapplication of the names of two Wiedemann (1830) species, *Coenosia torrida* and *Coenosia macularis*. The types of these species (in Copenhagen) are respectively female and male (though *macularis* was originally cited in error as female by Wiedemann), and Stein (1910c)—associating the two sexes—synonymised the names. But *P. torrida* (Wiedemann) possesses a submedian antero-dorsal seta on the mid tibia in both sexes which is absent in *P. macularis* (Wiedemann), and the female of the latter species has all yellow femora (instead of blackish-brown femora as in the female of *torrida*). Thus the two species are distinct. Stein (1915, 1918) referred a number of specimens from Formosa to *macularis*, and Hennig (1941) in his catalogue of the Diptera of Formosa (accepting Stein's and Seguy's (1937) synonymy of *macularis* with *torrida*) referred to the same material as *P. torrida* (Wiedemann). But neither name is correctly applied to this Formosan material (collected by H. Sauter and mainly in Berlin), which really belongs to *P. immaculipennis* described by Frey (1917). Likewise Hennig's (1952) reference to *P. torrida* (Wiedemann), and his figure of the male hypopygium, refers to *P. immaculipennis* Frey (the type of which is in Helsinki). *P. immaculipennis* is extremely closely allied to *P. torrida* and is the only other known species of *Pygophora* (apart from *P. confusa* Stein) possessing the submedian *ad* seta on the mid tibia, but it is easily distinguished from *torrida* in the female sex by having all yellow femora instead of blackish-brown femora (the males of the two species are very alike even in the genitalia). I have seen no true *P. torrida* (Wiedemann) or *P. macularis* (Wiedemann) from Formosa. It should be noted that Malloch (1929a, p. 345) also confused the species involved, and what he refers to as *immaculipennis* Frey is *macularis* Wiedemann and his *macularis* is really *torrida* Wiedemann.

Séguy (1937) listed *Atomogaster biseriata* Walker from Gilolo Island, Indonesia (=Halmahera Island), as a species of *Pygophora*. The type of *biseriata* Walker (in B.M. Nat.Hist.) has been examined and in spite of the very bad condition (head, abdomen and all legs missing and thorax badly rubbed) it is clear that it is not a *Pygophora* but belongs to the genus *Atherigona* Rondani. However, the type of *Atomogaster triseriata* Walker, described on the same page as *biseriata* (Walker 1862, p. 11), is also in the B.M. collection and is a true *Pygophora* synonymous

with *P. torrida* (Wiedemann); *triseriata* Walker was overlooked by Séguy (1937) and omitted from his catalogue of Muscidae in "Genera Insectorum".

The present work is concerned only with the taxonomy of adult flies since the immature stages of *Pygophora* are still unknown. Almost nothing is known of the behaviour of adult *Pygophora* other than that they are predacious in habit (as some other Coenosiinae) and feed on nematoceros Diptera and possibly other small insects. In the course of this study I have seen several pinned specimens of *Pygophora* with the shrivelled remains of psychodids and culicids between the fore legs or attached to the proboscis, and Paramonov (1961, p. 512) has recorded seeing specimens of the common Australian species *P. apicalis* Schiner bearing labels indicating that they were predatory on chironomids or mycetophilids. Emden (1940, p. 94) records a sciarid,? *Sciara flavoscutellata* Enderlein, as prey of *P. acromiata* (Speiser).

MATERIAL STUDIED

In addition to studying the material in the collection of the British Museum (Natural History) it has been possible, through the courtesy of the specialists mentioned in the Acknowledgments section, to study types and other specimens from the following Museum collections:

University Museum, Oxford (Oxf.d.Univ.Mus.); Muséum National d'Histoire Naturelle, Paris; Musée Royal de l'Afrique Centrale, Tervuren (Mus.R.Afr.Cent. Tervuren); Zoölogisch Museum, Amsterdam (Zool.Mus.Amsterdam); Zoologisches Museum der Humboldt-Universität, Berlin (Zool.Mus.Humb.Univ.); Deutsches Entomologisches Institut, Berlin (D.Ent.Inst.); Naturhistorisches Museum, Basel (Nat.Mus.Basel); Naturhistorisches Museum, Vienna; Museo Civico di Storia Naturale, Genoa; Universitetets Zoologiske Museum, Copenhagen; Naturhistoriska Riksmuseum, Stockholm; Museum Zoologicum Universitatis, Helsinki; Division of Entomology Museum, Canberra (Div.Ent.Mus.Canberra); School of Public Health and Tropical Medicine, Sydney (S.P.H.T.M.); Australian Museum, Sydney (Aust. Mus.); National Museum of Victoria, Melbourne (Nat.Mus.Vict.); United States National Museum, Washington (U.S.Nat.Mus.); Bernice P. Bishop Museum, Honolulu (Bishop Mus.).

The abbreviations given in brackets above are those used throughout the text in listing the material examined. British Museum (Natural History) is abbreviated B.M.Nat.Hist.

METHODS EMPLOYED

Most of the descriptions of species of *Pygophora* published hitherto omit mention of many important characters which are most helpful in species identification but often refer to characters which are common to all species, which are in fact generic; furthermore for the forty-six species (including synonyms) already described only five figures exist in the literature. Thus it has been necessary to redescribe all species and to present a full set of figures to assist in correct determination. In *Pygophora*, as in Muscidae generally, the male genitalia and associated structures are of the greatest value for the separation of most species but they have so far

been illustrated in only three species (Hennig, 1952). In the present work the male genitalia or associated structures such as the fifth sternite have been examined for each species; figures have been given in each case to reduce what would otherwise require complex description to a minimum. In addition to species descriptions I have attempted to give a diagnosis for each species but it should be appreciated that many species differ from all others in the genus only by combinations of characters which defy very succinct diagnosis.

All figures have been drawn with the aid of a camera lucida. Those of the male hypopygium are drawn from slide mounts, and in some cases hairs and bristles which in life stand out erect from the surface are pressed slightly flat; this should be borne in mind in connection with Figs. 79–90. For slide preparation the male genitalia were first treated in the usual way with cold 10 per cent. caustic potash.

Measurements of body length have been made with the fly viewed from the side with the arista and any bristles projecting apically from the abdomen omitted, i.e. from the leading edge of the antenna to the end of the last abdominal segment. Wing measurements are with the wing viewed flat and measured from the base of the tegula. The length of the third antennal segment relative to the second and the distance by which it falls short of the mouth-margin (epistome) have been measured with the fly viewed from the facial aspect with the third antennal segment horizontal.

Terms and abbreviations

In the keys and descriptions, terms and abbreviations are used as follows:

The two pairs of backwardly-directed setae on the frons are referred to (following Emden, 1940) as reclinate frontal setae (Figs. 1 and 2, *r.f.s.*) and the two pairs of inwardly-directed setae as inclinate frontal setae (Figs. 1 and 2, *i.f.s.*). To distinguish the more dorsal seta of each pair from the ventral one the words upper and lower are prefixed—thus upper reclinate frontal seta, etc. The reclinate and inclinate frontal setae are the setae *ors* and *ori* of Hennig (1960) respectively. In some species an extra pair of small inclinate setae occurs (Fig. 7) between the upper and lower pairs of inclinate frontal setae and each such extra seta is referred to as a supernumerary inclinate frontal seta.

Abbreviations of the thoracic setae are: *ph*, posthumeral seta; *post dc*, postsutural dorsocentral setae; *post ia*, postsutural intra-alar setae; *prst acr*, presutural acrostichal hairs; *prst dc*, presutural dorsocentral seta; *stpl*, sternopleural setae.

In describing the legs the convention of imagining the leg to be extended straight and at right-angles to the longitudinal axis of the fly is followed, and abbreviations for the positions of setae are: *a*, anterior; *ad*, antero-dorsal; *av*, antero-ventral; *d*, dorsal; *p*, posterior; *pd*, postero-dorsal; *pv*, postero-ventral; *v*, ventral.

For the abdomen and male hypopygium the terms employed are shown in Figs. 5 and 6. The apparent first tergite is well known to be composite and is T1 + 2; hence the fourth apparent tergite (last visible tergite in the female) is T5. In the male of *Pygophora* the sixth tergite is apparently undeveloped, and the large tergal plate lying between T5 and the epandrium of the hypopygium (which it is usually accepted represents T9) is evidently T7 + 8. This is clearly a compound tergite and bears an oblique superficially marked line which may be pre-

sumed to represent a line of fusion between T7 and T8. The large sclerite T7 + 8 often bears a transverse row of strong setae which appear to be discal in position, but careful examination shows that they always lie just anterior to the line of fusion between T7 and T8 and therefore that they are to be regarded as the marginal setae of T7. On the ventral surface of the abdomen the subgenital sternite (sternite 5) of the male is strongly developed and apico-laterally is produced into a large lobe on either side, referred to as the lateral lobes of sternite 5. In some species the lateral lobes of sternite 5 are extraordinarily complex and a suture occurs between the base of each lobe and the main body of the sternite; in these species (*P. cheesmanae* sp. n. and its allies from New Guinea) the lobes are apparently capable of movement independently of the rest of the sternite, and can, it appears, be infolded to the mid-line, probably playing an active part in mating. In describing the abdominal pattern the dark areas have been referred to as spots, although not always well defined; the dark areas in the mid-dorsal line are the median spots, and the rows of dark areas on either side are the sublateral spots. In reality the "spots" are areas from which the paler surrounding pollinosity is absent. Some species show traces of ventro-lateral spots on the lower sides of the tergites. In the figures showing dorsal views of the abdomen or lateral views of the whole abdomen the minor surface hairs have been omitted, only the principal setae being drawn (e.g. Figs. 33-36).

KEY TO THE GENERA OF ORIENTAL AND AUSTRALASIAN COENOSIINAE

For present purposes I am following the usual classification of Muscidae (e.g. as in Emden 1940, 1941) and regarding the Coenosiinae as a subfamily; Hennig (1956, 1960), in his new classification in course of publication, treats the group as a tribe, Coenosiini, of the Mydaeinae. Whatever status is accorded the group it forms one of the more easily definable supra-generic taxa in the Muscidae, characterised as follows: male head dichoptic, eyes as widely separated as in female, frons broad in both sexes; frons without cruciate interfrontal setae or proclinate frontal (orbital) setae, with one or two pairs of reclinate frontal setae; sternopleuron with three setae more or less arranged in an equilateral triangle; lower calypter diverging from margin of scutellum; wing with vein $Cu_{1b} + 1A$ (sixth vein) not nearly reaching hind margin; pteropleura bare.

The genera occurring in the Oriental and Australasian regions can be distinguished by the following key. It is worth noting that the Coenosiinae are absent from New Zealand, unless one accepts the endemic New Zealand genus *Limnohelina* Malloch as belonging in the group (as in Séguy, 1937); in this genus the lowest *stpl* seta is distinctly nearer to the upper posterior *stpl* seta than to the upper anterior one, and the reclinate frontal setae are directed slightly outward as well as backward towards the eyes (in all true Coenosiinae the reclinate setae are directed straight upwards and backwards without any inclination outwards). These characters of *Limnohelina*, combined with the presence of a well developed *ad* preapical seta on the hind tibia, place this genus in the Mydaeni (*sensu* Hennig, 1956, p. 103) and it is therefore excluded from consideration here.

Key to Genera

1. Head with only one pair of reclinate frontal (orbital) setae. Hind tibia usually with one *ad* seta, sometimes without..... 2
- . Head with two pairs of reclinate frontal setae. Hind tibia with two *ad* setae [Group 2 of Hennig]..... 3
2. Prescutum with dorsocentral setae very small, scarcely distinguishable from the setulose hairs. Fore femur without or with at most one or two *pv* setae preapically [Group 3 of Hennig]..... *Atherigona* Rondani
[type-species: *A. varia* (Meigen)]
- . Prescutum with a pair of very strong presutural dorsocentral setae. Fore femur with a complete row of long *pv* setae [Group 4 of Hennig] *Coenosia* Meigen
[type-species: *C. tigrina* (Fabricius)]
3. Mid tibia with one submedian *pd* seta. Frontal triangle large or at least long and narrow, more or less reaching the lunula..... 4
- . Mid tibia with two *pd* setae. Frontal triangle small and confined to the area of the ocelli, not nearly reaching the lunula..... 6
4. Scutellum with only two strong setae, the apical pair. Wings milky-white along posterior and apical margins, brown along anterior margin and elsewhere pale smoky-brownish. Hind tibia with only one very small inconspicuous submedian *pd* seta *Orchisia* Rondani
[type-species: *O. costata* (Meigen)]
- . Scutellum with four strong setae, a basal and an apical pair. Wings usually more or less hyaline, never partly milky-white. Hind tibia with two *pd* setae, the second one sometimes very small.. 5
5. Arista pubescent or short plumose, the same in both sexes..... *Lispocephala* Pokorný
[type-species: *L. alma* (Meigen)]
- . Arista long pectinate in male, very long plumose (pectinate in one species) in female *Pectiniseta* Stein
[type-species: *P. prominens* (Stein)]
6. Fore tibia with a strong submedian *pv* seta. Lowest *stpl* seta much shorter and finer than either of upper *stpl* setae. Upper inclinate frontal setae inserted much nearer to lower reclinate frontal setae than to lower inclinate frontal setae (Fig. 1). Arista very long plumose on basal half and bare on apical half, rarely sparsely plumose on basal four-fifths. Ocellar setae moderately well developed, always distinct..... *Pygophora* Schiner
[type-species: *P. apicalis* Schiner]
- . Fore tibia without a submedian *pv* seta. Lowest *stpl* seta long and strong, the upper anterior seta the shortest of the *stpl* setae. Upper inclinate frontal setae inserted nearer to lower inclinate frontal setae than to lower reclinate frontal setae (Fig. 2). Arista closely and regularly plumose to the apex, the hairs of medium length. Ocellar setae almost always minute and hair-like *Cephalispa* Malloch **stat. n.**
[type-species: *C. scutellata* Malloch]

In connection with the above key the following points should be made. A few species of *Caricea* R.-D., in the sense of Emden (1940), occur in the Oriental and Australasian regions and these will run to *Coenosia*; in accordance with Hennig (1961, p. 518) *Caricea* is here accepted as synonymous with *Coenosia*. *Pectiniseta* Stein is distinguishable from *Lispocephala* only by the key character given, and I am not at all sure that it can be upheld as a good genus. *Cephalispa* Malloch was

described (Malloch, 1935) as a subgenus of *Lispocephala* to include species differing from typical *Lispocephala* in possessing two (instead of one) *pd* setae on the mid tibia, a narrow frons and small frontal triangle. These are all characters shown by *Pygophora* and Emden (1942) alluded to *Cephalispa* as a subgenus of *Pygophora*. But several very important and constant characters distinguish *Cephalispa* from true *Pygophora*, the most important of these being the absence of the *pv* seta from the fore tibia; another character, hitherto overlooked, lies in the sternopleural setae as detailed in the key (cf. Figs. 3 and 4). Since *Cephalispa* is clearly and constantly separable from both *Lispocephala* and *Pygophora* by several good characters it is best regarded as a distinct genus transitional between the two (with the mid tibia of a *Pygophora* but the fore tibia of a *Lispocephala*) although on balance of characters undoubtedly closer to *Pygophora*.

The groups of Hennig referred to in the key are those recognised by him in "Die Fliegen der Palaearktischen Region" (1960, 1961).

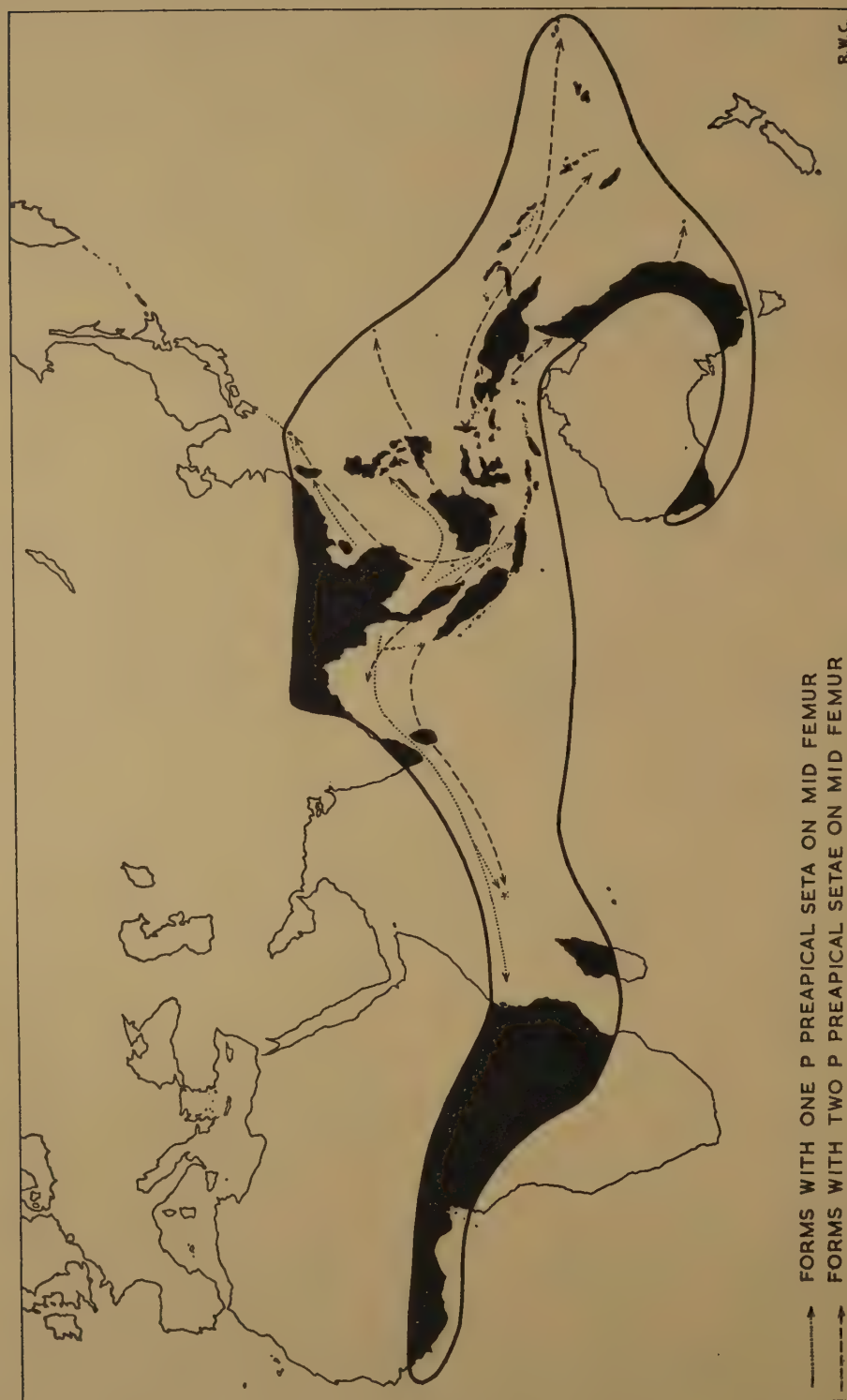
ZOOGEOGRAPHY OF PYGOPHORA SCHINER

Pygophora is a palaetropical genus with a distribution extending from Sierra Leone to Samoa; it does not occur within the confines of the Palaearctic Region and is absent from New Zealand. The fullest development of the genus is in the Indo-Malayan and Austro-Malayan subregions, particularly in New Guinea; over a third of the species of *Pygophora* are known to occur in New Guinea and the Bismarck Archipelago. Eight new species from New Guinea are described in this paper and doubtless others will be discovered as the fauna of the forested and mountainous interior becomes better known.

The species of *Pygophora* fall into two divisions, according to the presence of one or two *p* preapical setae on the mid femur of both sexes. It is hard to assess the significance of this character but it seems to represent a natural evolutionary cleavage and each division appears to be monophyletic (the recognition of two genera would not be unreasonable but is premature at present). Forms with a single preapical seta on the mid femur may have originated in south-east Asia and thence spread northwards towards Formosa and westwards to the Seychelles and Madagascar (from which a single endemic species is known) and Africa—all the Ethiopian species possess one preapical femoral seta only and show close affinity with species from Malaya and Burma. Forms with the single seta occur only, so far as is known, eastwards to Java, Borneo and the Philippines and are unknown from New Guinea, Australia and the Pacific.

On the other hand forms with two preapical setae on the mid femur appear to have radiated from a primary centre of evolution in the general area of Indonesia and New Guinea, and to have spread mainly eastwards and south-eastwards into the western Pacific and Australia; a few species occur in the mainland of southern Asia, and on Ceylon, but there are none in Africa (one species, *P. respondens* (Walker), the most widespread of all *Pygophora* species, has, however, reached the Seychelles).

Endemic island species occur in Fiji and the Samoa group and these are clearly derivatives of western Melanesian forms, conforming with the usual zoogeograph-



Map showing the approximate distribution of *Pygophora*. The arrows indicate in a generalised way the possible routes by which the genus has dispersed.

ical picture of an Austro-Malayan origin for the fauna of these islands. It is interesting to notice that *P. buxtoni* Malloch from Samoa resembles *P. hirtimana* Malloch of the Solomon Islands much more closely than it resembles *P. ctenophora* Bezzi from Fiji (though all three clearly belong to the same group), and it is tempting to see in this some support for Edwards' (1928) tentative conclusion, from his study of the Nematocera of the Pacific, that some at any rate of the insect fauna has reached Samoa by a route by-passing Fiji. A break at Fiji occurs in the known distribution of *P. hopkinsi* Malloch, though is perhaps due to incomplete collecting; *P. hopkinsi* occurs in the Philippines, Admiralty Islands, Solomon Islands, northern Queensland, and the New Hebrides and further east in Samoa but is apparently absent from Fiji.

Only eight species are known from the mainland of Australia but this small fauna is of two types, the one composed of endemic species with a wide distribution in eastern Australia (some extension into Western Australia) and the other occurring in northern Queensland and composed of non-endemic species derived from Indonesia and New Guinea. There is some overlap of the two faunae since at least two of the endemic species reach northwards into Queensland, and one of the endemic species (*P. minuta* Malloch) is only known from this territory. *P. compressiventris* (Thomson) (syn. *P. norrisi* Paramonov) and *P. maculigera* (Stein) (syn. *P. aliena* Malloch) are examples of Indonesian and New Guinea species which extend their range into Queensland; the names in synonymy were originally given to Queensland material. Another Queensland species, *P. argentea* Paramonov, is very closely allied to *P. nitidiventris* Malloch (with a known range from Malaya to Buru), and might perhaps be the same species—with the limited material at present known it is not possible to be certain about this. An endemic species occurs on Lord Howe Island (*P. howeana* Paramonov) and this has almost certainly been derived from the same stock as *P. majalis* Paramonov on the mainland of New South Wales. No species are yet known from Tasmania.

Pygophora is absent from West Pakistan and apparently from the central areas of India, as specimens have been seen only from southern peninsular India, Darjeeling and Assam. No material has been seen from East Pakistan but this may well be due to lack of collecting; on the other hand it is very low-lying country and the distribution of known *Pygophora* localities in south-east Asia generally suggests that in this area the genus may be associated with moderately high altitudes. Though there is always the possibility that this apparent association reflects the habits of the collectors rather than the insects.

The general distribution of *Pygophora* with an indication of possible lines of spread is shown on the accompanying map.

GENERIC DIAGNOSIS

Pygophora Schiner, 1868

Pygophora Schiner, 1868, *Nov. Reise, Diptera*: 295. Type-species: *Pygophora apicalis* Schiner, 1868, by original designation and monotypy.

Diplogaster Bigot, 1886, *Ann. Soc. ent. Fr.* (6) 6 Bull.: xiii. Type-species: *Diplogaster nigricauda* Bigot, 1886 [= *Pygophora macularis* (Wiedemann, 1830)], by monotypy. Generic synonymy with *Pygophora* first implied by Stein, 1907, *Z. Hym. Dipt.* 4: 280.

Diagnosis

♂♀. Head with two pairs of reclinate frontal (orbital) setae. Upper inclinate frontal setae inserted nearer to lower reclinate frontal setae than to lower inclinate frontal setae. Frons high and relatively narrow, frontal triangle small and not nearly reaching lunula. Arista very long-plumose on basal half, bare on apical half, very rarely long-plumose on basal four-fifths. Thorax with 1 + 3 dorso-central setae and usually a very small additional *dc* setula preceding *prst dc* seta. Prealar seta absent. Lowest sternopleural seta much smaller than either of upper sternopleural setae. Scutellum with four strong setae, a basal and apical pair (in one exceptional species basal pair reduced and hair-like). Fore tibia with a sub-median *pv* seta. Mid femur with one or two *p* preapical setae. Mid tibia with two *pd* setae. Hind tibia with one *av*, two *ad*, and two *pd* setae (♂ of *P. absentiseta* sp. n. exceptional in having only one *pd* seta).

Immature stages: unknown.

Distribution: Palaeotropics and Australia.

SPECIES-GROUPINGS

The species of *Pygophora* fall into two principal divisions, one in which there are two preapical setae on the posterior surface of the mid femur (Division A as referred to later), and the other in which there is only one seta in this position (Division B).

In several species of Division A the male possesses a preapical ventral lobe on the hind tibia, which (as mentioned in the Introduction) Stein considered to be the only generic character of *Pygophora*. Although this character is clearly not of generic significance it was at first thought that it did delimit a natural species-group; however, when its presence is correlated with other characters, particularly the structure of the male hypopygium and abdominal tergite 5, it becomes clear that not even species-group significance can be attached to the presence of the lobe.

In Muscidae generally some of the best morphological specific characters are provided by the male genitalia (indeed many species are only separable by genital characters), and close resemblance of the male hypopygium is usually good evidence of affinity. In *Pygophora* several different forms of the hypopygium exist and a particular pattern almost certainly indicates a natural species-group. Thus the close similarity (Figs. 79–84) of the ♂ hypopygium in *P. macularis*, *P. maculipennis*, *P. respondens*, *P. confusa*, *P. torrida* and *P. maculipennis* indicates their close affinity; of these species the first four possess the tibial lobe and the last two do not. On the other hand the tibial lobe also occurs in the male of *P. apicalis* and *P. intermedia*; the genitalia of these species are quite unlike those of *P. respondens* and its allies, and also quite different from one another. The lobe appears therefore to have arisen independently in different groups.

Taking male genital characters in conjunction with other characters it is possible to indicate some fairly distinct species-groups in Division A, but there is the usual residue of species of doubtful position whose affinities are not at all clear. The lines between groups are not hard and fast and I have not attempted to define

the groups by name or number; the arrangement of species in the descriptive section of this paper follows, however, the general groupings indicated below.

Division A species (2 *p* preapical setae on mid femur):

Group showing ♂ hypopygium with large broad paralobes shaped as in Figs. 79–84. Abdomen usually with T5 forming a strongly flattened dorsal keel bearing long outstanding flattened setae (generally as in Fig. 42). Hind tibia almost always with *pv* setae. Mid tibia sometimes with an *ad* seta. Species included: *P. respondens* (Walker), *P. setitarsis* Stein, *P. macularis* (Wiedemann), *P. maculipennis* Stein, *P. confusa* Stein, *P. torrida* (Wiedemann) and *P. immaculipennis* Frey.

In all the following groups the mid tibia is always without an *ad* seta.

Group showing ♂ hypopygium with long slightly clavate paralobes and long mesolobes (Figs. 85–90). T5 and T7 + 8 with long flattened setae or with scales or long fine upcurved hairs laterally, dorsum of T5 keel-like or subconical. Hind tibiae with *pv* setae (except in *luteicornis*).

Species included: *P. apicalis* Schiner, *P. maculigera* (Stein), *P. majalis* Paramonov, *P. caledonica* (Bigot), *P. absentiseta* sp. n., *P. howeana* Paramonov, *P. luteicornis* (Walker), *P. compressiventris* (Thomson), *P. hopkinsi* Malloch and *P. lepidofera* (Stein).

Group showing (♂) flattened scales on T4 as well as T5 and T7 + 8, and hypopygium as in Fig. 91.

Species included: *P. minuta* Malloch only.

In all the following groups the ♂ abdomen never has T5 strongly flattened and keel-like, at most slightly laterally compressed dorsally.

Group showing ♂ hypopygium with a long dense fringe of black hairs postero-basally on each paralobe, the paralobes of characteristic shape (Figs. 95–97).

Species included: *P. buxtoni* Malloch, *P. hirtimana* Malloch, *P. ctenophora* Bezzi; *P. intermedia* sp. n. is placed here also but the nature of the abdomen suggests some affinity with the first two groups above.

In all the following groups the ♂ hind tibia is always without *pv* setae, and the hind tibia is always without a preapical lobe.

Group in which ♂ has a characteristic furcate lateral lobe of sternite 5 as in Figs. 117 and 118. Antennae (♂) very long and nearly reaching mouth-margin. Supernumerary inclinate frontal setae present (♂♀). Femora dark brown, at least at extreme bases (♂♀).

Species included: *P. trimaculata* Karl, *P. keiseri* sp. n., *P. floresana* (Hennig).

Group with (♂) a peculiarly modified abdomen with the postabdomen very clearly set off from preabdomen. Paralobes of hypopygium extremely large and strongly clavate (Figs. 63–68).

Species included: *P. cheesmanae* sp. n., *P. dolabra* sp. n., *P. villicoxa* sp. n. Perhaps also *P. brandti* sp. n. should be placed here on the basis of the abdominal structure but the hypopygium is very different.

Group with (♂) a number of small bristles on the third antennal segment near the base of the arista.

Species included: *P. seticornis* sp. n. only.

Group (♂ and ♀) in which the fore tibia is without *ad* setae. Arista plumose on most of its length, only the apical fifth bare. Abdomen without the usual spots but with broad semi-shining dark transverse fasciae which fill most of the tergite. Supernumerary inclinate frontal setae present.

Species included: *P. nitidiventris* Malloch, *P. argentea* Paramonov, *P. flavida* sp.n.

Group with ♂ hypopygium as in Figs. 78 and 93, each paralobe bearing exteriorly a curious black socketed process. Frons unusually broad. Species included: *P. longipila* (Stein), *P. enigma* sp. n.

In the following Division A species the affinities are obscure and the species cannot be fitted into any of the species-groupings outlined above: *P. simplex* Hennig, *P. liturata* (Walker), *P. abnormalis* Paramonov, *P. bakeri* sp. n., *P. unicolor* (Stein), *P. xanthogaster* sp. n.

Division B (1 *p* preapical seta on mid femur):

Group with only two strong scutellar bristles, the basal pair reduced and hair-like. Humeral calli yellow but scutellum blackish in ground colour.

Species included: *P. microchaeta* sp. n. only.

Group with the normal four strong scutellar bristles. If humeral calli yellow then scutellum also yellow in ground colour.

Species included: all other Division B species, viz:—*P. pendleburyi* sp. n., *P. parvipuncta* (Stein), *P. vittigera* sp. n., *P. tumidiventris* (Stein), *P. pallens* (Stein), *P. nigromaculata* sp. n., *P. lutescens* Frey, *P. alemella* Séguy, *P. africana* sp. n., *P. acromiata* (Speiser), *P. pallipalpis* (Stein).

KEY TO THE SPECIES OF *PYGOPHORA* SCHINER

(1) Males

The male is unknown in *P. unicolor* (Stein), *P. nitidiventris* Malloch, and *P. xanthogaster* sp. n. and these species cannot be included in the key. Only a damaged male lacking the abdomen and genitalia has been seen in *P. bakeri* sp. n. and this species is omitted.

1. Oriental and Australasian species, including Seychelles and Madagascar 2
- . African species 46
2. Hind tibia with only one *pd* seta, the normal proximal *pd* seta absent *P. absentiseta* sp. n. (p. 446)
- . Hind tibia with the usual two *pd* setae 3
3. Mid femur with two *p* preapical setae. Abdomen sometimes with T5 produced into a prominent dorsal keel and hind tibia sometimes with a ventral preapical lobe 4
- . Mid femur with only one *p* preapical seta. Abdomen never with T5 produced into a prominent dorsal keel and hind tibia always without a preapical lobe 39

4. Hind tibia with a ventral preapical lobe (Fig. 13)..... 5
- Hind tibia simple, without a preapical lobe..... 11
5. Hind metatarsus with a short row of long fine hairs on antero-ventral surface (Fig. 23). Hind tibia without *pv* setae. Femora partly or largely blackish-brown. Abdomen mainly grey basally *P. setitarsis* Stein (p. 423)
- Hind metatarsus without long hairs on *av* surface. Hind tibia with one or more *pv* setae. Femora entirely yellow. Abdomen largely yellow or reddish-yellow basally..... 6
6. Mid femur on *av* surface with a series of very long strong curved spine-like setae followed by a row of very short curved spinous setulae (Fig. 9). Fore tibia without *ad* setae and with a distinct *pd* row of fine erect short hairs. Hind femur with a distinct *a* row of fine setae in addition to the *ad* and *av* rows..... *P. respondens* (Walker) (p. 420)
- Mid femur not armed as above on the *av* surface. Fore tibia with at least two distinct *ad* setae, all the hairs recumbent as usual. Hind femur without a row of *a* setae in addition to the *ad* and *av* rows..... 7
7. Mid tibia with a small submedian *ad* seta. Sides of T5 with an area of short stout upwardly-directed spinous setae (Fig. 44). Third antennal segment about 2.5 times as long as second segment and falling short of mouth-margin by about half its length. Face whitish pollinose *P. confusa* Stein (p. 430)
- Mid tibia without a submedian *ad* seta. Sides of T5 with long fine upcurved setae or hairs, usually slightly flattened. Third antennal segment long, from 3.8–5.5 times as long as second segment and only falling slightly short of mouth-margin. Face yellow pollinose..... 8
8. Mid femur with a regular comb of short stout spine-like setae on apical half of *av* surface (Fig. 10). Hind tibia with one submedian *pv* seta *P. macularis* (Wiedemann)
(p. 425)
- Mid femur without a comb of stout spine-like setae on the *av* surface. Hind tibia with two or three *pv* setae or with a series of *pv* setulae on apical half..... 9
9. Hind tibia with a series of about 7 or 8 down-curved *pv* setae of irregular length on the apical half (Fig. 14). Preapical lobe of hind tibia ending in large black tooth-like serrations (Fig. 14). T5 laterally with very numerous small fine upcurved hairs (Fig. 43)..... *P. apicalis* Schiner (p. 437)
- Hind tibia with two or three (rarely four) erect widely spaced *pv* setae. Preapical lobe of hind tibia bearing small black spinules but not ending in strong teeth. T5 laterally with not very numerous long slightly flattened setae which are only slightly upcurved 10
10. T5 dorsally forming a prominent laterally flattened keel. T4 and T5 with indistinct sublateral spots and T1 + 2 and T3 entirely yellow. Dorsum of T7 + 8 with numerous flattened setae which stand out on either side as in Fig. 42 *P. maculipennis* Stein (p. 428)
- T5 only slightly compressed dorsally, not forming a prominent narrow keel. T4 and T5 with large glossy blackish-brown sublateral spots and T1 + 2 and T3 reddish-yellow with a median reddish-brown area. Dorsum of T7 + 8 with a few very long

- setae which stand out in a radiating way somewhat similar to those on the dorsum of T5 (Fig. 41) *P. intermedia* sp. n. (p. 461)
11. Mid tibia with a submedian *ad* seta 12
- Mid tibia without a submedian *ad* seta 13
12. T5 with very small sublateral spots and the grey pollinose area between median and sublateral spot much wider than sublateral spot. T7 + 8 with well developed distinctly flattened dorso-lateral setae, lying below the dorsal marginal setae, which are conspicuous in dorsal view. Antero-apical corner of paralobe slightly angulate (Fig. 84). [Ceylon to Formosa] *P. immaculipennis* Frey (p. 434)
- T5 with sublateral spots well developed, silvery-grey pollinose area between median and sublateral spots about equal in width to sublateral spot. T7 + 8 with dorso-lateral setae, below the dorsal marginal setae, weakly developed, inconspicuous in dorsal view. Antero-apical corner of paralobe more evenly rounded (Fig. 83). [Indonesia and Philippines] *P. torrida* (Wiedemann) (p. 432)
13. Mid tibia with a row of well developed *pv* setae (Fig. 21). Apical half of hind femur with a *pv* row of long strong curved spine-like setae. Apex of abdomen as in Fig. 49, dorso-apical area of T7 + 8 strongly pointed *P. luteicornis* (Walker) (p. 451)
- Mid tibia without *pv* setae. Hind femur without strong *pv* spines. Abdomen with dorso-apical area of T7 + 8 rounded, never strongly pointed although sometimes slightly prominent 14
14. Hind tarsus with a posterior lobe on third segment bearing a long tuft of black hairs (Fig. 24). Mid tibia with a shallow notch on the antero-ventral surface near the base (Fig. 20). Hind tibia with two or three small *a* setae (Fig. 15) *P. hirtimana* Malloch (p. 463)
- Hind tarsus simple, without long hairs. Mid tibia without a notch near the base. Hind tibia without setae in a strictly *a* position 15
15. Abdomen as in Fig. 58, T4 quite bare laterally and T5 on each side with an area of short dense curved hairs. [Fiji Islands only] .. *P. ctenophora* Bezzi (p. 465)
- Abdomen not as in Fig. 58, sides of T4 always with some normal hairs and T5 differently bristled or haired [not known from Fiji] 16
16. Hind femur on *p* surface near the base with an area of short stubby black spinous setae (Fig. 27). The *pd* setae of mid tibia erect, subequal in length, very long and fine and about five times as long as tibial diameter, the distal one inserted at the middle of the tibia and the proximal one unusually near the base (Fig. 22). Dorsal (*d*) preapical seta of hind tibia very long and sinuous, equal in length to first two segments of hind tarsus together. [Samoa only] *P. buxtoni* Malloch (p. 467)
- Hind femur without such spines, only with the normal surface hairs. The *pd* setae of mid tibia not like this, much less than five times as long as tibial diameter (except in *brandti*), distal seta inserted slightly beyond middle. *d* preapical seta of hind tibia at most equal in length to hind metatarsus, almost always much shorter than hind metatarsus 17
17. Third antennal segment with several small bristles on antero-internal edge near base of the arista (Fig. 32). Prescutum with two very strong pairs of *prst acr* setae and with a very strong pair of *dc* setae preceding the usual single pair of *prst dc* setae .. *P. seticornis* sp. n. (p. 483)
- Third antennal segment normal, without bristles near base of the

- arista. Prescutum normal, only with *acr* hairs which at the most are only slightly developed as setulae, without a strong pair of *dc* setae in front of the *prst dc* setae although there may be a small setula developed in this position. 18
18. Sides of T4 (as well as T5 and T7 + 8) with scale-like setae (Fig. 54). Lateral lobe of sternite 5 shaped as in Fig. 54. Hypopygium as in Fig. 91. Very small species, length 3.4 mm. *P. minuta* Malloch (p. 459)
- . Sides of T4 without scale-like setae (though scales sometimes present on T5 and T7 + 8). Lateral lobe of sternite 5 not shaped as in Fig. 54. Hypopygium not as in Fig. 91. Usually larger species 19
19. Abdomen with T5 forming a prominent dorsal keel which is strongly laterally compressed or subconical, much higher than T7 + 8 in lateral view. T5 bearing long outstanding flattened setae or long erect upcurved hairs or scales, always with some specialised bristling of this type. Hind tibia with at least one *pv* seta (? *caledonica*), usually with two or four to five. 20
- . Abdomen of normal shape or if with postabdomen well set off from preabdomen T5 rounded dorsally. T5 not laterally compressed and keel-like or subconical dorsally, in lateral view at most only slightly higher than T7 + 8. T5 only with normal hairs and setae, without such specialised bristling. Hind tibia without *pv* setae 26
20. Parafrontals with a strong pair of supernumerary inclinate setae between the normal upper and lower pairs of inclinate frontal setae (as in Fig. 7). Dorsum of T5 prominent but slightly rounded subconical, not strongly laterally flattened and keel-like. [Lord Howe Island only]. *P. howeana* Paramonov (p. 449)
- . Parafrontals without supernumerary inclinate frontal setae, only with the normal two pairs of such setae. Dorsum of T5 keel-like, strongly and noticeably laterally flattened. [Not from Lord Howe Island]. 21
21. T5 densely bristled on ventro-apical areas and bearing horizontal setae or fine upcurved hairs laterally (Figs. 47 and 48). Hind tibia with two (rarely only one) distinct *pv* setae in the apical half (? *caledonica*). Larger species, length 5.2–5.5 mm. 22
- . T5 with the usual long setae or hairs on ventro-apical areas but not very densely bristled, sides of tergite bearing scales or very noticeably flattened lanceolate setae. Hind tibia with *pv* setae in basal half or with a series of small preapical *pv* setae. Small species, length 3.4 to 3.8 mm. 24
22. From New Caledonia only [♂ of this species not seen and placed here from description of Paramonov (1961)]. *P. caledonica* (Bigot) (p. 445)
- . Not from New Caledonia 23
23. T7 + 8 with a very dense tuft of ventro-apical setae (Fig. 48). Mid femur with an area of very small setulae at apex of *p/pv* surface (Fig. 26). T5 with long setae on dorsal keel not directed strongly downwards, and ventro-apical fringe not containing a few outstandingly long setae. T4 without a strongly developed lateral marginal seta *P. majalis* Paramonov (p. 443)
- . T7 + 8 with only a very sparse ventro-apical tuft of four or five setae (Fig. 47). Mid femur without such an area of setulae at apex of *p/pv* surface. T5 with the long setae on dorsal keel directed very strongly downwards, and ventro-apical fringe con-

- taining a few outstandingly long setae. T4 with a strongly developed lateral marginal seta, usually very long and conspicuous (Fig. 47)..... *P. maculigera* (Stein) (p. 440)
24. T5 laterally bearing a few very large dark brown leaf-like scales standing out from the surface (Fig. 53). Hind tibia in median third with a row of four long *pv* setae (Fig. 18)..... *P. lepidofera* (Stein) (p. 457)
- T5 laterally with very numerous outstanding flattened lanceolate slightly upcurved setae (slightly scale-like but not broad and leaf-like). Hind tibia with *pv* setae not arranged like this, with four or five short *pv* setae along its length..... 25
25. Third antennal segment about 3.7 times as long as second segment, only falling short of mouth-margin by about one-sixth of its length. Lateral lobe of sternite 5 shaped as in Fig. 108. T4 with large well marked dark reddish-brown or blackish-brown median and sublateral spots separated by grey pollinose areas. Face and parafacials usually bright yellow pollinose..... *P. hopkinsi* Malloch (p. 454)
- Third antennal segment about 2.4 times as long as second segment and falling short of mouth-margin by nearly half its length. Lateral lobe of sternite 5 shaped as in Fig. 109. T4 almost entirely yellowish, at most only with traces of yellowish-brown spots. Face and parafacials pale yellowish-white pollinose.... *P. compressiventris* (Thomson) (p. 452)
26. Thorax almost entirely pale reddish-yellow, scarcely at all pollinose, only with three brown lines on mesonotum which unite posteriorly into a brown prescutellar area. Hypopygium with very small paralobes as in Fig. 107, and lateral lobe of sternite 5 strongly upcurved as in Fig. 119..... *P. flavida* sp. n. (p. 488)
- Thorax densely grey or yellowish-grey pollinose over an entirely blackish or dark brown ground colour. Hypopygium not as in Fig. 107, sternite 5 not as in Fig. 119..... 27
27. Hind tibia with four or five small antero-dorsal setae in addition to the normal two strong *ad* setae and usually with some small semi-erect supernumerary *pd* setulae also (Fig. 19). Lateral lobe of sternite 5 as in Fig. 61, hypopygium as in Fig. 94..... *P. simplex* Hennig (p. 493)
- Hind tibia without supernumerary *ad* setae or *pd* setulae, only with the normal two strong *ad* and two strong *pd* setae. Lateral lobe of sternite 5 not as in Fig. 61, hypopygium not as in Fig. 94 28
28. Antennae very long, third segment from 5.6 to 6.8 times as long as second segment and almost reaching mouth-margin or falling only slightly short of it. Lateral lobe of sternite 5 with characteristic bifurcate form (Figs. 117 and 118). Femora mainly or partly blackish-brown, at least darkened reddish-brown at extreme base, not entirely yellow. Parafrontals with a pair of supernumerary inclinate setae between upper and lower pairs of inclinate frontal setae (Fig. 7)..... 29
- Antennae much shorter, from 2.0 to 3.8 times as long as second segment and falling short of mouth-margin by a fifth of its length or more (only by about one-eighth in *enigma*). Lateral lobe of sternite 5 not of this bifurcate form. Femora entirely yellow. Parafrontals with or without a pair of supernumerary inclinate frontal setae 31
29. Upper arm of lateral lobe of sternite 5 truncate at the apex (Fig. 118). Femora only darkened at extreme bases. [Formosa].... *P. trimaculata* Karl (p. 469)

- Upper arm of lateral lobe of sternite 5 strongly acuminate at the apex (Figs. 74 and 117). Femora blackish-brown on basal third or more, at least on fore femora. 30
- 30. Hypopygium with paralobes shaped as in Fig. 98. Femora with only basal third or half dark, sometimes only fore femora extensively blackish-brown. [Ceylon and S. India]. *P. keiseri* sp. n. (p. 473)
- Hypopygium as in Fig. 74. Femora blackish-brown on basal three-quarters, only apices yellow. [Indonesia] *P. floresana* (Hennig) (p. 472)
- 31. Lateral lobe of sternite 5 and shape of abdomen as in Fig. 69, hypopygium as in Fig. 70. Only a single median row of presutural acrostichal hairs, sometimes very slightly irregular. Very large species, length 7.6 to 7.8 mm. *P. brandti* sp. n. (p. 481)
- Lateral lobe of sternite 5, shape of abdomen and form of hypopygium not as in Figs. 69 and 70. Presutural acrostichal hairs in two rows (except in *dolabra*). Smaller species, length 3.4 to 6.7 mm. 32
- 32. Abdomen of extraordinary form with postabdomen distinctly set off from preabdomen or epandrium well set off from T7 + 8 (Figs. 63, 65 and 67). Hypopygium with very enlarged clavate paralobes (Figs. 64, 66 and 68). [New Guinea species]. 33
- Abdomen of normal shape, without such a bizarre form in which postabdomen is noticeably set off from preabdomen. Paralobes of hypopygium not very large and clavate. [New Guinea, Indonesia, Australia] 35
- 33. Mid coxa with a dense ventro-apical fringe of bristles (Fig. 25). Mid and hind femora ventrally in the basal half with long fine erect yellowish-brown hair. Third antennal segment dark brown or dark reddish-brown. Interfrontal area reddish-brown or dark orange-brown. Abdomen as in Fig. 63, hypopygium as in Fig. 64 *P. villicoxa* sp. n. (p. 477)
- Mid coxa without a dense ventro-apical fringe of bristles, only with the usual fine coxal setae. Mid and hind femora without such fine erect hair, only with the normal recumbent surface hairs in this position. Interfrontal area yellow or orange-yellow. Third antennal segment orange or orange-yellow. Abdomen of different form, hypopygium as in Fig. 66 or 68. 34
- 34. Parafrontals with a supernumerary pair of inclinate setae between the upper and lower pairs of inclinate frontal setae. T5 not nearly as long as three preceding tergites together; epandrium strongly rounded and set off from T7 + 8 but latter tergite not obviously set off from T5 (Fig. 65). Hypopygium as in Fig. 66, sternite 5 as in Fig. 124. *P. cheesmanae* sp. n. (p. 475)
- Parafrontals without a supernumerary pair of inclinate frontal setae. T5 about as long as the three preceding tergites together (Fig. 67), T7 + 8 well set off from T5 but epandrium less distinctly set off from T7 + 8. Hypopygium as in Fig. 68, sternite 5 as in Fig. 123. *P. dolabra* sp. n. (p. 479)
- 35. Fore tibia with two small *ad* setae. Hind tibia with the *d* preapical seta very long, about equal in length to hind metatarsus. Antennae very short, third segment only twice as long as second segment and falling short of mouth-margin by its own length. Lateral lobe of sternite 5 as in fig. 62. Larger species, length 5.9 to 6.6 mm. *P. abnormalia* Paramonov (p. 497)

- . Fore tibia without *ad* setae. Hind tibia with very short *d* preapical seta which at most is only half as long as hind metatarsus. Antennae with third segment at least 2.4 times as long as second and falling short of mouth-margin by appreciably less than its own length. Lateral lobe of sternite 5 of different shape. Small species, length 3.4 to 4.2 mm. 36
36. Mesonotum with very dense bright silver pollinosity, the silver appearance changing with the light so that from some angles the dark ground colour of the mesonotum is very evident. Interfrontal area also bright silver pollinose, so that the entire frons appears silver from most angles. Parafrontals with a pair of small supernumerary inclinate frontal setae. Abdomen (Fig. 34) without spots, posterior tergites almost completely semi-shining brownish-black, only narrowly paler along anterior margins. Lateral lobe of sternite 5 as in Fig. 116. *P. argentea* Paramonov (p. 486)
- . Mesonotum with the usual dull greyish or slightly brownish pollinosity, ground colour not very evident from any angle. Interfrontal area yellow to dark brown, only very indistinctly whitish pollinose in some lights. Parafrontals without supernumerary setae. Abdomen with very large dark median and sublateral spots as usual, separated by grey pollinose areas, such spots present at least on T4 and T5. Lateral lobe of sternite 5 differently shaped 37
37. Hind femur with a row of four or five strong subequal *pv* setae in basal half (Fig. 28). Arista plumose on basal two-fifths, hairs on ventral side very short and inconspicuous. Paralobes of hypopygium strongly tapering in lateral view (Fig. 77), with a ridge on outer edge basally which bears strong blunt, black teeth directed inwards, inner surface medially also with three prominent teeth (Fig. 92). Frons of usual *Pygophora* proportions, rather high and narrow *P. liturata* (Walker) (p. 495)
- . Hind femur with one very long obvious *pv* seta at about a third from the base with a very fine inconspicuous seta on one or both sides of this. Arista plumose on most of its length on upper side, lower hairs well developed (Fig. 29). Paralobes of hypopygium not of this form, without such teeth, outer surface bearing a curious curved flattened black socketed process (Figs. 78 and 93). Frons unusually broad. 38
38. Antennae almost entirely dark brown, only very narrowly orange on extreme base of segment 3 and dorsally on segment 2; third segment about 3.8 times as long as second segment and only falling short of mouth-margin by about an eighth of its length. Interfrontal area brownish-orange or dark brown. *P. enigma* sp. n. (p. 491)
- . Antennae entirely yellow-orange, third segment about 2.8 times as long as second segment and falling short of mouth-margin by about a quarter of its length. Interfrontal area deep yellow *P. longipila* (Stein) (p. 490)
39. Lower parafrontals with some small setulose hairs between the inclinate setae and the eye-margin (Fig. 8), and with two pairs of supernumerary inclinate setae between the usual upper and lower pairs of inclinate frontal setae. Abdomen with basal tergites mainly blackish in ground colour with dense grey or yellowish pollinosity, sometimes also with black spots. [Seychelles and Madagascar only]. *P. pallipalpis* (Stein) (p. 522)

- . Lower parafrontals without setulose hairs between the inclinate setae and the eye-margin, and without supernumerary setae between the upper and lower pairs of inclinate frontal setae. Abdomen with basal tergites pale yellowish or reddish-yellow. [Not from Seychelles or Madagascar]..... 40
40. Scutellum with only two strong setae (apical pair), the basal pair very small and hair-like. Humeral calli yellowish but scutellum blackish in ground colour and concolorous with scutum..... *P. microchaeta* sp. n. (p. 503)
- . Scutellum with the usual four strong setae, basal pair as strong as apical pair. Humeral calli and scutellum yellowish (except in *pendleburyi*)..... 41
41. Humeral calli and scutellum blackish in ground colour and concolorous with prescutum and scutum. Fore tibia without *ad* setae. Very small species, length 3.8 mm..... *P. pendleburyi* sp. n. (p. 505)
- . Humeral calli and scutellum yellowish in ground colour and contrasting with darker reddish-brown or blackish ground colour of prescutum and scutum. Fore tibia with two small *ad* setae, rarely inconspicuous. Larger species, length 4.7 to 6.0 mm.... 42
42. Abdomen short and rather rounded, unusually broad and ovate in dorsal view (Fig. 35) with T3 and T4 short. Lateral lobe of sternite 5 narrow and tapering, more or less acuminate (Fig. 115)..... *P. pallens* (Stein) (p. 511)
- . Abdomen longer and subcylindrical, not at all rotund. Lateral lobe of sternite 5 not shaped as in Fig. 115 43
43. Antennae exceptionally short, third segment only about 1.8 times as long as second segment and falling short of mouth-margin by its own length or more. Lateral lobe of sternite 5 small and inconspicuous, shaped as in Fig. 59. Epandrium unusually large (Fig. 59). Abdomen with a median dark vitta (Fig. 33).. *P. vittigera* sp. n. (p. 508)
- . Antennae not exceptionally short, third segment 2.4 to 2.6 times as long as second segment and falling short of mouth-margin by half or three-fifths of its length. Lateral lobe of sternite 5 large and conspicuous, of different form. Abdomen usually without a definite median vitta 44
44. Sternite 5 extremely large, not very deeply incised in ventral view, in lateral view as in Fig. 60. Paralobes of hypopygium long and narrow, straight and rather evenly tapering (Fig. 60).... *P. nigromaculata* sp. n. (p. 513)
- . Sternite 5 smaller and very deeply incised ventrally (as in Fig. 122), in lateral view as in Fig. 110 or 111. Paralobes of hypopygium shorter, less regularly straight and tapering..... 45
45. Lateral lobe of sternite 5 rounded (Fig. 110). Hypopygium as in Fig. 106. [Java]..... *P. tumidiventris* (Stein) (p. 509)
- . Lateral lobe of sternite 5 as in Fig. 111. Hypopygium as in Fig. 104. [India and Ceylon] *P. lutescens* Frey (p. 514)
46. Humeral calli and scutellum with blackish ground colour, concolorous with prescutum and scutum. Mentum brown. Hypopygium with very long paralobes which bear strong blunt black spinules on outer surfaces (Fig. 100). Small species, length about 4.4 mm. *P. parvipuncta* (Stein) (p. 506)
- . Humeral calli and scutellum yellow in ground colour, contrasting with darker reddish-brown or blackish prescutum and scutum. Mentum yellow. Hypopygium with paralobes slightly less elongate and not bearing such spinules on outer surfaces. Larger species, length 5.7 to 7.0 mm..... 47

47. Mid femur on apical third of *pv* surface with dense irregular black setulae (Fig. 12). Hypopygium with paralobes shining black or blackish-brown and slightly backwardly curved (Fig. 101).. *P. acromiata* (Speiser) (p. 519)
- Mid femur without dense setulae on *pv* surface. Hypopygium with paralobes pale brown or reddish-yellow..... 48
48. Presutural *dc* seta inserted nearer to anterior margin of prescutum than to the transverse suture, almost on a level with the *ph* seta, and not preceded by a small *dc* setula (Fig. 30). Paralobes of hypopygium concave on anterior surfaces and slightly curved forwards, not swollen apically (Fig. 102)..... *P. alemella* Séguy (p. 516)
- Presutural *dc* seta inserted nearer to the transverse suture than to the anterior margin of the prescutum, distinctly behind the level of the *ph* seta, and preceded by a very small but distinct *dc* setula (Fig. 31). Paralobes of hypopygium convex on anterior surfaces and slightly curved backwards, somewhat swollen and rounded apically (Fig. 103)..... *P. africana* sp. n. (p. 518)

(2) Females

The female is unknown in the following species and cannot be included in the key: *P. enigma* sp. n., *P. longipila* (Stein), *P. luteicornis* (Walker), *P. majalis* Paramonov, *P. microchaeta* sp. n., *P. seticornis* sp. n., *P. trimaculata* Karl and *P. tumidiventrif* (Stein). The female of *P. microchaeta* however may be presumed to possess only two strong scutellar bristles as in the male, and this character will distinguish it from all other known species. Certain females can at present only be doubtfully associated with males, and in cases of doubtful association the specific name is preceded in the key by a question-mark. A number of females have been seen which cannot be associated at all with known males and may represent undescribed species; such females have been keyed out as “? sp. n.” where appropriate.

1. Oriental and Australasian species, including Seychelles and Madagascar..... 2
- African species..... 45
2. Mid tibia with a submedian *ad* seta..... 3
- Mid tibia without a submedian *ad* seta..... 6
3. Femora blackish-brown except for yellow apices..... *P. torrida* (Wiedemann) (p. 432)
- Femora entirely yellow..... 4
4. Third antennal segment distinctly brownish in apical half..... *P. confusa* Stein (p. 430)
- Third antennal segment more or less entirely yellow..... *P. immaculipennis* Frey (p. 434)
5. Mid femur with one *p* preapical seta..... 6
- Mid femur with two *p* preapical setae..... 11
6. Parafrontals with supernumerary inclinate setae between the normal upper and lower pairs of inclinate frontal setae, and with some small setulose hairs between inclinate frontal setae and eye-margin (Fig. 8). Prescutum with four or five rows of acrostichal hairs. Abdomen all dark, blackish with grey or yellowish pollinosity and usually some black spots. [Seychelles and Madagascar only]..... *P. pallipalpis* (Stein) (p. 522)

- Parafrontals without supernumerary setae or setulose hairs. Prescutum with two rows of acrostichal hairs. Abdomen largely pale, yellowish or reddish-yellow especially basally. [Not from Seychelles or Madagascar]..... 7
- 7. Humeral calli and scutellum grey. Fore tibia without *ad* setae. Mentum red-brown ? *P. pendleburyi* sp. n. (p. 505)
- Humeral calli and scutellum yellowish. Fore tibia with (usually two) small *ad* setae. Mentum yellow..... 8
- 8. Antennae exceptionally short, third segment only about 1.75 times as long as second segment and falling short of mouth-margin by much more than its own length..... *P. vittigera* sp. n. (p. 508)
- Antennae not exceptionally short, third segment about 2.0 to 2.4 times as long as second segment and falling short of mouth-margin by its own length or only a little more..... 9
- 9. Abdomen almost entirely yellow, without median spots (or with only a trace of such spots) and without evident grey pollinosity. Sublateral spots of T4 and T5 very small, T3 with only a faint trace of very small widely separated brownish sublateral spots *P. lutescens* Frey (p. 514)
- Abdomen with more extensive dark marking, with some evident median spots and some grey pollinosity, T3 with more definite and extensive dark marking..... 10
- 10. T4 with very large red-brown sublateral spots which are more or less coalesced with the median spot, only very narrowly grey pollinose between, the sublateral spots more than half as long as the tergite. T3 with the median and sublateral spots coalesced into a bold red-brown mark (Fig. 38) with only a very thin trace of grey pollinose lines *P. nigromaculata* sp. n. (p. 513)
- T4 with small brown sublateral spots which are separated by wide grey pollinose areas from the median brown spot, the sublateral spots less than half as long as the tergite. T3 with spots indistinct, sublateral spots well separated from median spot..... *P. pallens* (Stein) (p. 511)
- 11. Femora largely or partly blackish-brown or dark reddish-brown.. 12
- Femora entirely yellow or reddish-yellow..... 24
- 12. Abdomen entirely shining blackish-brown or very dark mahogany brown, without spots or pollinose areas. Thorax unicolorous dark blackish-brown or very dark reddish-brown, mesonotum semi-shining and non-pollinose (appearing black to naked eye). Interfrontal area dark velvety reddish-black or dark brown... *P. unicolor* (Stein) (p. 501)
- Abdomen and thorax not entirely blackish-brown or very dark brown, the abdomen with spots or obvious pollinose areas and the thorax grey or yellowish-grey pollinose (mesonotum not semi-shining and not appearing black to naked eye). Interfrontal area yellow to brick-red..... 13
- 13. Parafrontals with a supernumerary pair of inclinate setae between the normal upper and lower pairs of inclinate frontal setae (Fig. 7). T1 + 2 grey, usually brownish medio-dorsally..... 14
- Parafrontals without supernumerary inclinate setae. T1 + 2 largely or partly reddish-yellow, only rarely more or less all grey 15
- 14. Femora blackish-brown on basal three-quarters. Third antennal segment almost entirely pale brown, only yellow on basal quarter. Interfrontal area brick-red..... *P. floresana* (Hennig) (p. 472)
- Femora only blackish-brown on basal half or third. Third anten-

- nal segment mainly orange-yellow, only faintly tinged with brown. Interfrontal area orange or reddish-orange. [Differences given in this couplet may not be constant]..... *P. keiseri* sp. n. (p. 473)
15. Very small species, length 3.6 to 4.2 mm..... 16
 -. Larger species, length 5.5 to 7.1 mm..... 17
16. Parafrontals silvery-grey pollinose, ground colour blackish and contrasting with yellowish parafacials; silvery appearance of parafrontals contrasting with the orange interfrontal area.... *P. lepidofera* (Stein) (p. 457)
 -. Parafrontals yellowish pollinose, ground colour concolorous with that of parafacials; yellowish parafrontals not strongly contrasting with orange interfrontal area..... *P. hopkinsi* Malloch (p. 454)
17. Femora dark reddish-brown on basal two-fifths only, over half their length yellow..... 18
 -. Femora blackish-brown on basal four-fifths or more, only apices yellow (rarely only brown on basal two-thirds)..... 19
18. T1 + 2 and T3 glossy reddish-yellow, each with only a large median red-brown area. [Philippine Islands]..... *P. intermedia* sp. n. (p. 461)
 -. T1 + 2 and T3 almost entirely very dark reddish-brown with thin grey pollinosity, T3 with traces of two longitudinal pollinose lines dividing the dark brown colour into median and sublateral areas. [Malaya] ? sp. n.
19. T1 + 2 grey with dark brown median area, not at all reddish-yellow or yellowish. Tibiae brownish..... ? *P. setitarsis* Stein
 -. T1 + 2 largely yellowish or pale reddish-yellow, at least laterally. Tibiae yellow, at most only partly more reddish-brown..... 20
20. Fore coxae reddish-yellow, very inconspicuously white pollinose 21
 -. Fore coxae reddish-brown or dark brownish and grey pollinose... 22
21. Wings faintly tinged yellowish. Mesonotal pollinosity yellowish. Larger species, length 7.1 mm. [New Britain] ? sp. n.
 -. Wings clear hyaline. Mesonotal pollinosity grey or slightly yellowish-grey, not obviously yellowish to naked eye. Smaller species, length 5.5 to 6.1 mm. [New Guinea]..... ? *P. absentiseta* sp. n.
22. Mid femur with setae of *av* row very regular, without one conspicuously longer and stronger seta near the middle, the setae becoming gradually smaller towards the apex and those in the apical half not very strongly recumbent and hair-like. Sublateral spots of T3 and T4 rounded and not reaching sides of the tergite, limited externally by greyish pollinose areas. [Common and widespread species]..... *P. respondens* (Walker) (p. 420)
 -. Mid femur on *av* surface near the middle with a conspicuous seta which is longer and stronger than the other *av* setae, the setae beyond this strong seta rather hair-like and recumbent and much weaker than the erect *av* setae basad of the strong seta. Sublateral spots either small and limited by pollinose areas externally, or very large and extending round to ventral surfaces of the tergites 23
23. Sublateral spots of T3 and T4 small and not reaching sides of tergites, delimited exteriorly by pollinose areas, all median and sublateral spots well separated and surrounded by extensive yellowish-grey pollinose areas. Femora brown only on basal two-thirds. Tibiae yellow. [Formosa]..... ? *P. maculipennis* Stein
 -. Pollinose areas of abdomen very small and inconspicuous, sublateral "spots" extending round the sides of the tergites to the

- ventral surface or filling most of the dorsum of the tergites with shining dark brown areas. Femora blackish-brown except at extreme apices. Tibiae slightly and partially darkened reddish-brown. [Malaya, Java]..... ? sp. n.
24. Fore tibia without *ad* setae. Arista plumose on more than half its length (except in *liturata*)..... 25
- . Fore tibia with two or three small *ad* setae. Arista as usual, only plumose on basal third or two-fifths..... 28
25. Thorax pale reddish-yellow, scarcely at all pollinose, only with three brown longitudinal lines on mesonotum which unite to form a brown prescutellar area *P. flavida* sp. n. (p. 488)
- . Thorax blackish or very dark brown and grey pollinose, mesonotum without such a pattern 26
26. Parafrontals without a supernumerary pair of inclinate setae. Arista plumose only on basal third. Abdomen with very distinct brown median and sublateral spots on T3, T4 and T5 which are separated by grey pollinose areas. Mesonotum and scutellum densely grey pollinose and appearing grey from any angle, ground colour not distinctly visible when viewed from behind. *P. liturata* (Walker) (p. 495)
- . Parafrontals with a pair of supernumerary inclinate setae (sometimes small) between upper and lower pairs of inclinate frontal setae. Arista plumose on most of its length, only bare on about the apical quarter or fifth. Abdomen without spots, T4 and T5 (sometimes also T3) almost entirely rather shining dark reddish-brown, the tergites only narrowly yellow on margins, almost completely without obvious grey pollinosity. Mesonotum and scutellum only thinly grey pollinose so that when viewed from behind the dark brown or blackish ground colour is easily visible..... 27
27. Interfrontal area mostly very dark purplish-brown, only orange or reddish-orange near the lunula. Frons of normal width, not unusually broad. [Queensland]..... *P. argentea* Paramonov (p. 486)
- . Interfrontal area entirely pale orange-yellow or yellow. Frons unusually broad. [Indonesia, Malaya]..... *P. nitidiventris* Malloch (p. 485)
28. Abdomen entirely orange-red, without spots and with only a very thin trace of silvery pollinosity medially on last two tergites, the pollinosity most inconspicuous *P. xanthogaster* sp. n. (p. 502)
- . Abdomen not entirely orange-red, with median and sublateral spots and extensive conspicuous pollinose areas on most tergites 29
29. T4 with a pair of very strong erect median discal setae standing close together near the anterior margin and on the median spot. Abdominal pattern as in Fig. 37. [Philippine Islands]..... *P. bakeri* sp. n. (p. 499)
- . T4 without median discal setae (except in *simplex* in which a small fine pair is present but not near anterior margin of the tergite). Abdominal pattern not exactly as in Fig. 37. [Usually not from Philippine Islands]..... 30
30. Hind tibia with some small supernumerary *ad* setae in addition to the normal two strong *ad* setae, and usually with some supernumerary *pd* setulae in addition to the normal two strong *pd* setae. T4 with a transverse row of fine discal setae (Fig. 39)... *P. simplex* Hennig (p. 493)
- . Hind tibia without extra *ad* setae or *pd* setulae. T4 without a transverse row of discal setae..... 31

31. Parafrontals with a well developed supernumerary pair of inclinate setae between the normal upper and lower pairs of inclinate setae, so that there are three pairs of inclinate frontal setae.... 32
 -. Parafrontals without supernumerary inclinate setae..... 34
32. Third antennal segment dark brown. Interfrontal area dark reddish medially but blackish on the side margins:..... *P. villicoxa* sp. n. (p. 477)
 -. Third antennal segment orange-yellow or pale orange. Interfrontal area all orange-yellow or reddish-orange, not noticeably darkened at the sides..... 33
33. T1 + 2 mainly reddish-yellow. Sublateral spots of T3 and T4 small, T5 without a definite median mark and only darker brownish pollinose in the mid-line. Mentum very dark, brownish-black. [Lord Howe Island] *P. howeana* Paramonov (p. 449)
 -. T1 + 2 predominantly grey, only very narrowly and indistinctly yellowish. Sublateral spots of T3 and T4 larger, T5 with a very definite broad black median longitudinal line. Mentum yellow-brown. [New Guinea] *P. cheesmanae* sp. n. (p. 475)
34. Very small species, length 3.7 to 4.4 mm..... 35
 -. Medium-sized or large species, length 5.5 to 7.4 mm..... 36
35. T3 mostly yellow without grey pollinosity and without a median spot, only with a pair of small, indefinite reddish-brown sublateral spots. Parafrontals pale yellow pollinose, not strongly contrasting in colour with interfrontal area. Face and parafacials yellowish-white pollinose. Mid and hind coxae yellow..... *P. compressiventris* (Thomson) (p. 452)
 -. T3 mostly dark with very large bold blackish-brown median and sublateral spots separated by grey pollinose areas. Parafrontals grey pollinose and contrasting in colour with interfrontal area. Face and parafacials greyish pollinose. Mid and hind coxae reddish-brown with grey pollinosity *P. minuta* Malloch (p. 452)
36. T1 + 2 darkened dorsally with a large brown median mark or extensively and indefinitely brownish or blackish, not entirely reddish-yellow or yellow 37
 -. T1 + 2 entirely yellowish or reddish-yellow..... 39
37. Acrostichal hairs in two well separated rows. Wings entirely clear hyaline. Mentum dark brown or blackish-brown. T5 yellowish-brown pollinose in the mid-line, without a definite elongate black median spot. *pd* setae of mid tibia short and about one and a half and two times as long as tibial diameter. Setae of extensor surface of hind tibia not very long and not at all sinuous. [Ceylon to Java]..... *P. macularis* (Wiedemann) (p. 425)
 -. Acrostichal hairs in a single median row, sometimes slightly irregular presuturally. Wings with a brownish clouding apically. Mentum brownish-yellow or yellow-brown. T5 with a broad bold black elongate median spot. *pd* setae of mid tibia long and about three and a half to five times as long as tibial diameter. Some setae of extensor surface of hind tibia very long and slightly sinuous. [New Guinea]..... 38
38. Mesonotum with broad well marked black *dc* vittae easily visible in most lights. Face and parafacials dirty yellowish-white pollinose..... *P. brandti* sp. n. (p. 481)

- Mesonotum with only very narrow and inconspicuous blackish *dc* lines, scarcely at all visible in most lights. Face and parafacials bright yellow pollinose *P. dolabra* sp. n. (p. 479)
- 39. Antennae unusually short, third segment only twice as long as second segment and falling short of mouth-margin by its own length or more. Abdominal spots very small and very widely separated. T5 with several irregular erect short strong discal setae. T4 with a close-set row of strong erect marginal setae.. *P. abnormalis* Paramonov (p. 497)
- Antennae not unusually short, third segment 2.75 to 3 times as long as second segment and falling short of mouth-margin by much less than its own length. Abdominal spots large and not very widely separated. T5 without numerous irregular discal setae, at most with the normal one or two pairs of regular fine lateral discals. T4 with a sparser row of erect strong marginal setae, usually with only a strong pair of median marginals.... 40
- 40. Species from New Caledonia..... *P. caledonica* (Bigot) (p. 445)
- Species not known from New Caledonia..... 41
- 41. T4 with a transverse row of several strong erect marginal setae, not with only a single median pair of such setae. [Australia]... *P. apicalis* Schiner (p. 437)
- T4 with only a single pair of strong erect median marginal setae, otherwise hind margin of the tergite only with fine recumbent marginal hairs..... 42
- 42. T3 with median and sublateral spots coalesced into a single bold red-brown mark with only a faint trace of pollinosity distinguishing the spots. [Samoa]..... *P. buxtoni* Malloch (p. 467)
- T3 with median and sublateral spots distinct from one another or at least clearly separated by pollinose areas. [Not from Samoa] 43
- 43. T4 almost entirely grey except for the blackish-brown spots, not yellowish basally and only narrowly yellowish apically. T3 with the grey pollinose areas between the spots at least as long as the spots themselves..... *P. maculigera* (Stein) (p. 440)
- T4 broadly yellowish or reddish-yellow on basal and apical margins with grey pollinosity and dark spots confined to median two-thirds of the tergite. T3 with grey areas between median and sublateral spots shorter than the spots themselves so that the dark median area of the tergite appears constricted between the spots..... 44
- 44. Species from Fiji..... *P. ctenophora* Bezzi (p. 465)
- Species from Solomon Islands and Bismarck Archipelago..... *P. hirtimana* Malloch (p. 463)
- 45. Humeral calli and scutellum blackish in ground colour with grey pollinosity, concolorous with prescutum and scutum. Mentum brown..... *P. parvipuncta* (Stein) (p. 506)
- Humeral calli and scutellum yellowish in ground colour, much paler than the prescutum and scutum. Mentum yellow..... 46
- 46. Presutural dorsocentral seta (*prst dc*) inserted nearer to the anterior margin of the prescutum than to the transverse suture, about on a level with the *ph* seta, and not preceded by a small additional *dc* setula (Fig. 30) *P. alemella* Séguy (p. 516)
- Presutural dorsocentral seta (*prst dc*) inserted at the middle of the prescutum or nearer the transverse suture than the anterior margin, distinctly behind the level of the *ph* seta, and preceded by a very small but distinct additional *dc* setula (Fig. 31).... 47
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- Large species, length 6.3 to 7.8 mm..... *P. acromiata* (Speiser) (p. 519)

DESCRIPTIONS OF THE SPECIES

DIVISION A

Pygophora respondens (Walker, 1860)

Coenosia respondens Walker, 1860, *J. Proc. Linn. Soc.* 4: 142. Holotype ♀, CELEBES. In the British Museum (Natural History), London.

Coenosia (*Pygophora*) *lobata* Stein, 1900, *Természetr. Füzet.* 23: 147. Lectotype ♂, SINGAPORE. In the Zoologisches Museum der Humboldt-Universität, Berlin. Synonymy with *respondens* recognised by Stein (1901, p. 218), but the name *lobata* always subsequently used by Stein.

Pygophora semilutea Malloch, 1921, *Ann. Mag. nat. Hist.* (9) 7: 422. Holotype ♂, CEYLON. In the British Museum (Natural History), London. **Syn. n.**

Lectotype designation for C. lobata Stein: *C. (Pygophora) lobata* Stein was described from three syntypes, a ♂ from Singapore and a ♂ and a ♀ from New Guinea. The ♂ from Singapore has been selected and labelled as lectotype. The whereabouts of the New Guinea syntypes is not known to me: Stein gives "Friedr. Wilh. Hafen".

Diagnosis

♂. Mid femur with a row of strong curved *av* spine-like setae (Fig. 9), fore tibia with a close-set row of short erect *pd* hairs and without *ad* setae, hind tibia with preapical lobe. ♀ with blackish-brown femora, unusually regular row of subequal *av* setae on mid femur, no submedian *ad* seta on mid tibia, T1 + 2 yellowish, sublateral spots of abdomen not reaching sides of tergites and delimited exteriorly by pollinose areas on the dorsum.

Description

♂. *Head:* occiput pale grey pollinose. Interfrontal area yellow or yellow-orange. Face and parafacials yellowish-white pollinose. Ocellar setae fine, about equal in length to, but a little finer than, upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae pale yellow-orange, third segment about 3.5 times as long as second segment and falling short of mouth-margin by about a quarter of its length; arista long-plumose on about the basal half. Palpi pale creamy-yellow. Mentum reddish-brown. *Thorax:* ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae, mesonotum and scutellum all pale grey pollinose, the mesonotum with only a narrow trace of dark *dc* vittae in certain lights. Pre-sutural acrostichal hairs in two rows; the *dc* setula preceding the *prst dc* seta indistinct; two long fine *post ia* setae present. *Wings:* entirely hyaline, without trace of preapical dark suffusion. Calyptrae white with white fringes. Halteres pale yellow. *Legs:* entirely yellow except for mid and hind coxae which are reddish with grey pollinosity. Fore femur with one of the rows of posterior hairs developed into a distinct *p* row of strong setae similar to the *pd* and *pv* rows; fore tibia with the *pv* seta short, distinctly shorter than distance from its insertion to apex of tibia, with a continuous row of fine close-set erect *pd* hairs but without *ad* setae. Mid femur with two preapical *p* setae, with a series of long strong curved

av spine-like setae followed by small spinules (Fig. 9), and with a row of fine curved *pv* hairs on apical half; mid tibia without an *ad* seta, the two *pd* setae short and only one and one and three-quarter times as long as tibial diameter. Hind femur with a distinct *a* row of fine setae in addition to the *ad* and *av* rows, the *pv* surface with two long fine subequal submedian setae and a very small fine seta nearer to the base; hind tibia with a ventral preapical lobe and with one submedian *pv* seta, the *d* preapical seta much shorter than hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 45): laterally compressed towards the apex, T5 forming a prominent flattened dorsal keel, lateral lobes of sternite 5 large and rounded. T1 + 2 and T3 yellow without dark marking, or sometimes T3 with a narrow longitudinal median dorsal reddish-brown mark; T4 yellowish on the sides, with large well-marked reddish-brown median and sublateral spots, silvery-grey pollinose between the spots and outside the sublateral spots; T5 and T7 + 8 reddish-black in ground colour and pale grey pollinose, without spots but dorsal keel of T5 dark brown and only very lightly pollinose, hind margin of T5 narrowly yellowish. Venter, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. T5 with long slightly flattened setae standing out from the dorsal keel and with many long fine upwardly-directed hairs dorso-laterally, the ventro-apical margins with long backwardly-directed setae; T7 + 8 dorso-laterally with long fine upwardly-directed hairs similar to those on T5 and with some stronger slightly flattened setae dorsally. Hypopygium as in Fig. 82, each paralobe fringed with long inwardly-directed hairs on the outer margin and with short bristly hairs at the apex of inner surface. *Measurements*: body length 5.5 mm (range 5.2 to 5.8 mm), wing length 4.9 mm (range 4.5 to 5.1 mm) [20 specimens].

♀. All femora blackish-brown on basal three-quarters, yellow only at the apices. *Abdomen* with T1 + 2 pale reddish-yellow with a darker median mark; T3 only narrowly yellowish on basal and apical margins and ventrally, with large well marked reddish-brown or blackish-brown median and sublateral spots and with less distinct large brown ventro-lateral spots, the spots separated by grey pollinose areas; T4 similar to T3 with large red-brown or blackish-brown median, sublateral and ventro-lateral spots separated by grey pollinose areas, but only very narrowly yellowish on posterior margin; T5 grey pollinose with a well developed pair of blackish-brown sublateral spots and with a pair of large black-brown spots ventrally, median dorsal line with traces of yellowish-brown pollinosity. Median spots of T3 and T4 elongate and more or less parallel-sided, reaching from anterior margin of tergite to the marginal setae, the sublateral spots of these tergites not extending laterally around the sides of the tergite but small and limited exteriorly by grey pollinose areas. T4 without median discal setae, T5 almost always with a strong pair of median discal setae in addition to the pair of discal setae standing on or outside the sublateral spots. Fore femur without distinct *p* setae, fore tibia without erect *pd* hairs and with two *ad* setae, mid femur with an unusually regular row of subequal *av* setae in which there is no longer seta near the middle, hind femur without a distinct *a* row of setae, hind tibia without preapical lobe or *pv* setae. Mesonotum with distinct traces of three brownish vittae. *Measurements*: body length 5.7 mm (range 5.5 to 6.1 mm), wing length 5.0 mm (range 4.7 to 5.3 mm) [15 specimens].

Affinities

P. respondens belongs in one of the groups in which the ♂ has a preapical lobe on the hind tibia and a dorsal keel on T5 but is easily distinguished from other species in these groups by the characters given in the key and the diagnosis above.

Material examined

Coenosia respondens Walker, holotype ♀, CELEBES: Makassar, — (A. R. Wallace). *Coenosia (Pygophora) lobata* Stein, lectotype ♂, SINGAPORE: 1898 (Biro). *Pygophora semilutea* Malloch, holotype ♂, CEYLON: Kandy, 21.v.1892 (Yerbury). SEYCHELLES: 1 ♀, Mahé, 1908–9 (J. S. Gardiner) (B.M.Nat.Hist.); 1 ♂, Cousin Island, 30.iii.1952 (E. S. Brown) (B.M.Nat.Hist.). CEYLON: 1 ♂ Sudugunga, 2.vii.1919 (—) (B.M.Nat.Hist.); 1 ♂, Kandy, 3.ii.1953 (F. Keiser) (Nat.Mus. Basel); 4 ♀♀, Kandy, 15.xi.1953, 28.xii.1953, 3.ii.1954, 1.iii.1954 (F. Keiser) (Nat. Mus. Basel); 2 ♀♀, Kandy, Hantana, 23.xii.1953 (F. Keiser) (Nat.Mus. Basel); 1 ♀, Haragama, 30.xii.1953 (F. Keiser) (Nat.Mus. Basel); 3 ♂♂, —, 1882 (Stamforth Green) (Oxf. Univ. Mus.). GOA: 1 ♀, Mormugao, — (J. C. Bridwell) (U.S. Nat. Mus.). THAILAND: 1 ♀, Sungkie, 7.i.1902 (H. C. Robinson and N. Annandale) (B.M.Nat.Hist.); 1 ♀, Chiangmai, Fang, 500 m., 15.iv.1958 (T. C. Maa) (Bishop Mus.). CHRISTMAS ISLAND [Indian Ocean]: 2 ♂♂, 1 ♀, Christmas Island, — (C. W. Andrewes) (B.M.Nat.Hist. and U.S. Nat. Mus.); 2 ♀♀, Christmas Island, 1.iv.1933 (B.M.Nat.Hist.). SUMATRA: 1 ♂, 3 ♀♀, Fort de Kock, 1925 (E. Jacobson) (U.S. Nat. Mus.); 1 ♀, Sabang Isles, ii.1938 (L. E. Cheesman) (B.M.Nat.Hist.); 1 ♀, Simeulue Island, Sibigo, viii.1913 (E. Jacobson) (Zool. Mus. Humb. Univ.). JAVA: 1 ♂, Batavia, 1–7.vii.1906 (—) (B.M.Nat.Hist.); 2 ♀♀, Batavia, xii.1907 (Jacobson) (Zool. Mus. Humb. Univ.); 1 ♂, —, vii. (—) (Zool. Mus. Humb. Univ.); 1 ♀, Goenoeng Gedeh, iii.1911 (E. Jacobson) (Zool. Mus. Humb. Univ.); 1 ♂, Goenoeng Gedeh, iii.1911 (E. Jacobson) (U.S. Nat. Mus.); 1 ♂ Buitenzorg, iii.1907 (F. Muir) (Bishop Mus.); 3 ♀♀, Buitenzorg, — (F. Muir) (Bishop Mus.). CELEBES: 2 ♂♂, 2 ♀♀, Makassar, iv.1908 (F. Muir) (Bishop Mus.). BRITISH NORTH BORNEO: 1 ♂, W. Coast Residency, Ranau, 500 m., 28.ix. to 7.x.1958 (T. C. Maa) (B.M. Nat. Hist.); 1 ♀, W. Coast Residency, Ranau, 500 m., 28.ix. to 7.x.1958 (T. C. Maa) (Bishop Mus.); 1 ♂, W. Coast Residency, Ranau, 8 mls. N. of Paring Hot Springs, 500m., 8–11.x.1958 (T. C. Maa) (Bishop Mus.); 1 ♀, Singkor, 19.i.1959 (T. C. Maa) (Bishop Mus.). PHILIPPINE ISLANDS: 1 ♂, Luzon, Manila, xi.1914 (—) (U.S. Nat. Mus.); 1 ♂, 1 ♀, Los Banos, — (P. I. Baker) (U.S. Nat. Mus.); 1 ♂, Los Banos, 10.xi.1915 (F. Muir) (Bishop Mus.); 1 ♂, 3 ♀♀, Mindanao, Surigao, — (Baker) (U.S. Nat. Mus.); 2 ♂♂, Manila, xii.1924 (R. C. McGregor) (U.S. Nat. Mus.); 1 ♀, Manila, xi.1924 (R. C. McGregor) (U.S. Nat. Mus.); 2 ♀♀, Negros, Cuernos Mountains, — (Baker) (U.S. Nat. Mus.); 1 ♀, Luzon, Mt. Makiling, — (Baker) (U.S. Nat. Mus.); 1 ♂, Sulu, Tarawaka, 12.ii.1957 (Yoshio Kondo) (Bishop Mus.). DUTCH NEW GUINEA: 1 ♂, Saonek [islet off Waigeo Island], 23.i.1910 (M. de Beaufort) (Zool. Mus. Humb. Univ.); 1 ♂, Vogelkop, Danowaria, 2.vi.1919 (J. L. Gressitt) (Bishop Mus.); 1 ♀, Waris, S. of Hollandia, 450–500m., 27–30.vi.1959 (T. C. Maa) (Bishop Mus.). N.E. NEW GUINEA: 1 ♀, Maprik, 150m., 29.xii.1959 to 17.i.1960 (T. C. Maa) (Bishop Mus.). NEW GUINEA (PAPUA): 2 ♀♀, Port Moresby, vi–vii.1917 (Strong) (S.P.H.T.M.). NEW BRITAIN: 1 ♀, Rabaul, Keravat, 10.vii.1934 (J. L.

Froggatt) (B.M.Nat.Hist.). ADMIRALTY ISLANDS: 1 ♀, Manos, 1932 (*N. E. H. Caldwell*) (B.M.Nat.Hist.); 1 ♀, Manus, 10.ix.1932 (*J. L. Froggatt*) (B.M.Nat.Hist.). SOLOMON ISLANDS: 1 ♀, Guadalcanal, Lunga, 11.iii.1935 (*R. A. Lever*) (B.M.Nat.Hist.); 2 ♀♀, Neal Island, Vunelua, 8.viii.1934 (*R. A. Lever*) (B.M.Nat.Hist.); 1 ♀, Three Sisters, Malaupaina, 10.v.1934 (*R. A. Lever*) (B.M.Nat.Hist.); 1 ♀, Tulagi, 12.viii.1936 (*R. A. Lever*) (B.M.Nat.Hist.); 1 ♀, Tulagi, i.1933 (*R. A. Lever*) (B.M.Nat.Hist.); 1 ♀, Tulagi, 23.vii.1933 (*R. J. A. W. Lever*) (B.M.Nat.Hist.); 1 ♀, Santa Isabel, Papari, 27.ii.1934 (*R. J. A. W. Lever*) (B.M.Nat.Hist.); 1 ♀, Santa Isabel, Huleo, 27.ii.1934 (*R. J. A. W. Lever*) (B.M. Nat.Hist.); 1 ♂, 1 ♀, Russell Island, Sanata, 22.ii.1934 (*R. J. A. W. Lever*) (B.M.Nat.Hist.); 1 ♀, Rennell Island, Hutuna, 16.xi.1953 (*J. D. Bradley*) (B.M.Nat.Hist.). NEW HEBRIDES: 1 ♂, Malekula, Ounua, iii-iv.1929 (*L. E. Cheesman*) (B.M.Nat.Hist.); 3 ♀♀, Malekula, Ouna, ii.1929 (*L. E. Cheesman*) (B.M.Nat.Hist.). FORMOSA: 1 ♀, Lambeh Island, ii.1908 (*H. Sauter*) (U.S.Nat.Mus.); 1 ♂, Lambeh Island, ii.1908 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 2 ♂♂, Alikang, vi.1909 (*H. Sauter*) (U.S.Nat.Mus.); 1 ♂, Paiwan District, Paroe, viii.1912 (*H. Sauter*) (U.S.Nat.Mus.); 1 ♂, Kankau, ix.1912 (*H. Sauter*) (D.Ent. Inst.); 1 ♂, 2 ♀♀, Koshun, iii.1908 and i.1909 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 3 ♀♀, Takao, 9.viii.1907 and 19.x.1907 (*H. Sauter*) (U.S.Nat.Mus.); 4 ♂♂, 7 ♀♀, Takao, 29.iii. to 20.xi.1907 (*H. Sauter*) (Zool.Mus.Humb.Univ.). GUAM: 2 ♂♂, 2 ♀♀, Guam Island, — (*D. T. Fulloway*) (U.S.Nat.Mus.); 1 ♀, Togcha, Guam Mts., 9.v.1945 (—) (U.S.Nat.Mus.). HAWAII [introduced by aircraft]: 1 ♀, Honolulu, 4.vii.1944 (—) (U.S.Nat.Mus.).

Distribution

P. respondens is the most widespread species of *Pygophora*, occurring from the Seychelles eastwards to the New Hebrides, on the mainland of south-east Asia, and north-eastwards to Formosa and Guam. Under the name *lobata* Stein literature references to the occurrence of *P. respondens* are given by Stein (1910b), Bezzi (1923), Emden (1940), and Hennig (1941) for Seychelles; Malloch (1922) and Hennig (1941) for Christmas Island; Stein (1915, 1918), and Hennig (1941) for Formosa; Stein (1909, 1920b) for Java and Sumatra; Stein (1920b) for Saonek; Stein (1919b) for Bivak Island (= Biak); and Hennig (1952) for Sumbawa and Flores (Indonesia). Almost all these records are based on material examined and listed above, and those which are not (i.e. the records of Stein, 1919b and Hennig 1952) are certainly based on correctly identified specimens. It is curious, but worth mentioning here because of the references to *lobata* in the literature, that very shortly after describing *lobata* Stein recognised its synonymy with *respondens* Walker (see Stein, 1901, p. 218); nevertheless in all Stein's subsequent papers he referred to the species by the name *lobata*.

Pygophora setitarsis Stein, 1919

Pygophora setitarsis Stein, 1919, *Nova Guinea* 13: 211. Holotype ♂, DUTCH NEW GUINEA. In the Zoölogisch Museum, Amsterdam.

Diagnosis

♂. Hind tibia with a preapical lobe and without *pv* setae, hind metatarsus with a row of long curved hairs, femora partly darkened.

Description

♂. *Head*: occiput grey pollinose. Interfrontal area deep orange. Face and parafacials thickly golden-yellow pollinose. Ocellar setae strong, only a little smaller than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright yellow-orange, third segment about 3.5 times as long as second segment and probably falling short of mouth-margin by about one quarter of its length [head of holotype badly crushed and no other ♂ seen]; arista long-plumose on basal two-fifths. Palpi pale yellow. Mentum dark reddish-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; densely grey pollinose with traces of three yellowish-brown mesonotal vittae, scutellum dark brown and only very thinly dusted on a median basal triangular area. Presutural acrostichal hairs in two or three irregular rows, but three pairs of presutural *acr* setulae distinctly developed; the *dc* setula preceding the *prst dc* seta distinct and almost as large as the *acr* setulae; two strong *post ia* setae present. *Wings*: entirely hyaline, without trace of apical dark suffusion. Calyptrae white with creamy-white fringes. Halteres pale yellow. *Legs*: [mid legs of holotype missing] coxae reddish-brown with grey pollinosity, fore femora dark brown on basal quarters and yellow on apical three-quarters, hind femora dark brown on basal three-quarters and yellow apically [mid femora probably brown basally], tibiae and tarsi yellow, fore tarsi brownish dorsally. Fore tibia with the *pv* seta very long, distinctly longer than distance from its insertion to apex of tibia, and with two *ad* setae. [Mid femur probably with two preapical *p* setae]. Hind femur with only one very long *pv* seta at about one third from the base; hind tibia with a ventral preapical lobe but without any *pv* setae; hind metatarsus with a short comb of black spinules ventrally at the base and with a ventral sub-basal series of seven long curved hairs (Fig. 23). *Abdomen*: laterally compressed towards the apex with T5 produced into a dorsal keel, lateral lobes of sternite 5 very large. Tergites dark reddish-brown in ground colour with grey pollinosity, the hind margins of T1 + 2, T3 and T4 narrowly yellowish, T7 + 8 blackish-brown; T3 and T4 with dark reddish-brown median and sublateral spots, and T5 with dark brown sublateral spots and dorsal keel. Venter reddish-brown, lobes of sternite 5 deep yellow-brown. T5 dorsally with a series of long outstanding flattened setae, those on the keel directed backwards and slightly downwards, and ventro-apically with a marginal row of long fine setae, laterally with outstanding but short and slightly curved and slightly flattened setae; T7 + 8 with long curved slightly flattened setae. Sternite 5 with a pair of small flattened processes at the base, each lateral lobe with the ventral margin produced into a short truncate process. *Measurements*: approximate only, holotype in bad condition: body length 5.5 mm, wing length 5.2 mm.

♀. Not definitely known because of the difficulty of correct association with the ♂. Almost certainly with blackish-brown femora and possibly with brownish instead of yellow tibiae, abdomen probably all dark in ground colour with large blackish-brown spots and grey pollinosity, T1 + 2 not pale.

Affinities

P. setitarsis is probably most closely related to *P. respondens* (Walker). The

curious regular row of a few long fine hairs on the hind metatarsus distinguishes *setitarsis* from all other species.

Material examined

Holotype ♂, DUTCH NEW GUINEA: Bivak Island (= Biak Island), ii.1910 (——).

In addition one ♀ has been seen which may belong to this species: NEW GUINEA: Minjemfluss, —— (*R. Schlechter*) (U.S.Nat.Mus.).

Distribution

Known only from the New Guinea type locality, possibly widespread in New Guinea.

Pygophora macularis (Wiedemann, 1830)

Coenosia macularis Wiedemann, 1830, *Auss. Zweifl. Ins.* 2: 438. Holotype ♂ [not ♀ as given by Wiedemann], "OSTINDIEN" (? = INDONESIA). In the Universitetets Zoologiske Museum, Copenhagen.

Diplogaster nigricauda Bigot, 1886, *Ann. Soc. ent. Fr.* 6 Bull.: xiv. Holotype ♂, CEYLON. In the British Museum (Natural History), London. Syn. n.

Diagnosis

♂. With a regular comb of short stout spines on the *av* surface of mid femur and a preapical lobe on hind tibia.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area deep yellow or orange-yellow. Face and parafacials heavily golden-yellow pollinose. Ocellar setae about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae deep yellow-orange, third segment about 3.8 to 4.0 times as long as second segment and falling short of mouth-margin by about one-sixth or one-seventh of its length; arista long-plumose on basal two-fifths. Palpi yellowish-white. Mentum red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, mesonotum and scutellum yellowish-grey pollinose with almost no trace of mesonotal vittae. Presutural acrostichal hairs in two rows; the *dc* setula preceding *prst dc* seta indistinct; two distinct *post ia* setae present. *Wings*: entirely hyaline in some specimens, but usually with a dark brown suffusion near the apex of R_{2+3} which extends backwards to R_{4+5} or a little beyond. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for mid and hind coxae which are reddish or blackish with grey pollinosity. Fore tibia with the *pv* seta strong, about equal in length to the distance from its insertion to apex of tibia, and with two *ad* setae. Mid femur with two preapical *p* setae, with a comb of short strong spines on the apical half of *av* surface (Fig. 10), and with a similar comb of short spines on the apical half of *pv* surface, the last few longer and stronger than the others; mid tibia without an *ad* seta, the two *pd* setae about one and one and a half times as long as tibial diameter. Hind femur with two very long *pv* setae in basal half; hind tibia with a ventral preapical lobe and with a single submedian *pv* seta, the *d* preapical seta short and only a little over half as long as hind meta-

tarsus; hind tarsus simple. *Abdomen* (Fig. 46): laterally compressed towards the apex, T5 forming a strongly flattened dorsal keel, lateral lobes of sternite 5 large and subtriangular. T1 + 2 and T3 yellow without spots or with a trace of a median red-brown mark on T3; T4 yellowish laterally and dorsally on the posterior margin with dark brown median and sublateral spots separated by pale silvery-grey pollinose areas; T5 reddish-brown in ground colour with pale grey pollinosity and with faint traces only of sublateral spots, very rarely yellowish on apical margin; T7 + 8 reddish-black with grey pollinosity. Venter, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. T5 with very long backwardly-directed flattened setae on the dorsal keel and with numerous long upcurved slightly flattened setae laterally, ventro-apical margin with a tuft of very long setae some of which are extremely long and sinuous and longer than the others; T7 + 8 with numerous long outstanding curved setae similar to those on T5. Hypopygium as in Fig. 80, paralobes large and broad, each with a dense fringe of inwardly-directed hairs on the posterior margin and with a few fine backwardly-directed hairs at extreme base. *Measurements*: body length 5.5 mm (range 5.1 to 5.9 mm), wing length 4.8 mm (range 4.3 to 5.1 mm) [20 specimens].

♀. Femora yellow as in ♂, but wing without preapical dark suffusion. Abdomen with T1 + 2 reddish-yellow with a blackish-brown median mark and extensive grey pollinosity which partly obscures the ground colour; T3 and T4 mainly greyish with distinct blackish-brown median and sublateral spots, the hind margins of the tergites reddish-yellow; T5 with distinct black-brown sublateral spots and a faint trace of a brownish median vitta, also with traces of a pair of dark ventro-lateral spots as on T4. T4 without median discal setae, T5 without median discal setae in addition to the lateral discal setae on the sublateral spots. Mid femur without strong ventral rows of spines; hind femur with three long subequal *pv* setae in basal three-fifths; hind tibia without preapical lobe and without *pv* seta. Mesonotum with distinct traces of dark *dc* vittae. Third antennal segment about 2.5 times as long as second and falling short of mouth-margin by more than half its length. *Measurements*: body length 5.9 mm (range 5.5 to 6.3 mm), wing length 5.2 mm (range 4.9 to 5.4 mm) [18 specimens].

Affinities

P. macularis belongs in a group with the compressed and keeled fifth tergite and in which some species have the lobed hind tibia; it is very closely allied to *P. maculipennis* Stein but is distinguished by the comb of short spines on the antero-ventral surface of the mid femur and by having only one submedian *pv* seta on the hind tibia instead of two or three as in *maculipennis*.

Material examined

Coenosia macularis Wiedemann (labelled "*Anthom. macularis* W."), holotype ♂, without locality label but Wiedemann (1830) gives "Ostindien" which probably indicates Indonesia. *Diplogaster nigricauda* Bigot, holotype ♂, CEYLON (no other data). CEYLON: 1 ♂, Hingurakgoda, 20.xii.1953 (*F. Keiser*) (S.P.H.T.M.); 1 ♀, Hingurakgoda, 20.xii.1953 (*F. Keiser*) (Nat.Mus.Basel); 3 ♂♂, Teldeniya, 13.i.1954 (*F. Keiser*) (Nat.Mus.Basel and Div.Ent.Mus.Canberra); 1 ♀, Teldeniya, 16.xi.1953

(*F. Keiser*) (Nat.Mus.Basel); 2 ♀♀, Teldeniya, 20.i.1954 (*F. Keiser*) (Nat.Mus. Basel); 1 ♀, Kandy, Deiyannewela, 17.x.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Kandy, Deiyannewela, 18.i.1954 (*F. Keiser*) (Nat.B.M.Nat.Hist.); 1 ♂, Kandy, Deiyannewela, 25.ii.1954 (*F. Keiser*) (B.M.Nat.Hist.); 1 ♂, 2 ♀♀, Kandy, Roseneath, 29.ix.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Kandy, Roseneath, 11.viii.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♂, Kandy, L. Blake's Drive, 16.xii.1953 (*F. Keiser*) (Nat.Mus.Basel); 2 ♂♂, Kandy, 3.ii.1954 (*F. Keiser*) (Nat.Mus.Basel and B.M.Nat. Hist.); 4 ♀♀, Kandy, 20.xi.1953, 3.iii.1954, 6.ii.1954 (*F. Keiser*) (Nat.Mus.Basel); 1 ♂, Peradeniya, Botanical Gardens, 20.v.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Peradeniya, Exper. Stat., 4.xi.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♂, 1 ♀, Hara-gama, 30 and 31.xii.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♂, Mallapitiya, 3.xi.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Balakuduwa, 18.xii.1953 (*F. Keiser*) (Nat.Mus. Basel); 2 ♂♂, Suduganga, 29.v.1919 (—) (B.M.Nat.Hist.); 1 ♂, Suduganga, 9.xi.1918 (B.M.Nat.Hist.); 1 ♂, Suduganga, 20.iv.1922 (—) (B.M.Nat.Hist.); 6 ♀♀, Suduganga, 18–30.v.1919 (—) (B.M.Nat.Hist.); 1 ♂, Trincomalee, Hot Wells, 27.vii.1890 (*Yerbury*) (B.M.Nat.Hist.); 1 ♀, Trincomalee, 2.i.1892 (*Yerbury*) (B.M.Nat.Hist.); 1 ♀, 1 ♀, Colombo, 14.vi.1891 (*Yerbury*) (B.M.Nat.Hist.); 6 ♂♂, 4 ♀♀, —, 1882 (*Stamforth Green*) (Oxf.d.Univ.Mus.) INDIA: 1 ♂, Darjeeling District, Ghumti, vii.1911 (*F. H. Gravely*) (B.M.Nat.Hist.); 1 ♂, S. Malabar, Walayar Forests, 28–29.viii.1953 (*P. S. Nathan*) (B.M.Nat.Hist.); 1 ♀ Coimbatore, viii.1953 (*P. S. Nathan*) (B.M.Nat.Hist.). THAILAND: 1 ♂, Doi Sutep, (*D. and E. Thurman*) (U.S.Nat.Mus.); 2 ♂♂, 1 ♀, Chiangmai, Fang, 500m. and Chiangdao, 450 m., 5–19.iv.1950 (*T. C. Maa*) (Bishop Mus.). MALAYA: 1 ♂, Pahang, Fraser's Hill — (—) (U.S.Nat.Mus.); 2 ♂♂, Pahang, Fraser's Hill, 25 and 26.i.1929 (*H. M. Pendlebury*) (B.M.Nat.Hist.); 1 ♂, Perak, Larut Hills, 10.ii.1932 (*H. M. Pendlebury*) (B.M.Nat.Hist.). SUMATRA: 1 ♂, Kahan Djahe, x.1936 (U.S.Nat.Mus.). JAVA: 1 ♂, Buitenzorg, 24.ii to 12.iii.1904 (*K. Kraepelin*) (B.M.Nat.Hist.).

Distribution

Widespread in south-east Asia eastwards to Java. Stein (1915, 1918) has recorded *P. macularis* (Wiedemann) from certain localities in Formosa, but it is probable that this was due to misidentification. I have seen much of the material (Sauter collection, partly in D.Ent.Inst. and partly in Zool.Mus.Humb.Univ.) on which Stein based the Formosan records and it all belongs to *Pygophora immaculipennis* Frey. In this species there is an *ad* seta on the mid tibia as in *P. torrida* (Wiedemann); in *P. macularis* this seta is absent. Stein (1910c) incorrectly synonymised *torrida* and *macularis* of Wiedemann, and this has led to some confusion in identification. I have seen no true *macularis* (conspecific with Wiedemann's type) from Formosa, although the very closely related *P. maculipennis* Stein occurs there, and material identified as *macularis* from Formosa is really *immaculipennis* Frey described in 1917. The two males and two females from Ceylon and collected by Lt.-Col. Yerbury, which are listed above, have been referred to in the literature as *P. maculipennis* Stein by Malloch (1922, p. 382). *P. maculipennis* is so closely allied to *macularis* that it might be considered a subspecies of the latter; but the type locality of *maculipennis* (Krakatau) lies within the range of *macularis* and

in the absence of allopatry it seems preferable to regard the two forms as distinct, but very close, species.

Pygophora maculipennis Stein, 1909

Pygophora maculipennis Stein, 1909, *Tijdschr. Ent.* 52: 271. Lectotype ♂, KRAKATAU ISLANDS. In the Zoölogisch Museum, Amsterdam.

Lectotype designation: *P. maculipennis* was described from three ♂ syntypes from Krakatau. I have selected and labelled one of these, in Amsterdam, as lectotype. Another of the syntypes (in Zool.Mus.Humb.Univ.) has been labelled paralectotype. I have not seen the third syntype.

Diagnosis

♂. Recognised by combination of the following characters: hind tibia with preapical lobe, T5 with a flattened dorsal keel, mid tibia without *ad* seta, mid femur without comb-like *av* spines, hind tibia with 3–4 *pv* setae.

Description

♂. *Head:* occiput pale grey pollinose. Interfrontal area deep yellow or orange-yellow. Face, parafacials and parafrontals densely golden yellow pollinose. Ocellar setae fine, but equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright yellow-orange, third segment long and about 4.7 to 4.9 times as long as second segment, falling short of mouth-margin by about one eighth or one-tenth of its length; arista long-plumose on basal half. Palpi pale yellowish. Mentum light red-brown. *Thorax:* ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, sometimes slightly yellowish-grey on mesopleura, mesonotum and scutellum pale yellowish-grey pollinose, mesonotum with almost no trace of dark vittae. Presutural acrostichal hairs in two rows; the *dc* setula preceding *prst dc* seta indistinct, usually a little smaller than *acr* hairs; two well developed *post ia* setae present. *Wings:* usually with an elongate dark brown mark on apex of R_{2+3} , but dark spot sometimes absent so that the wing is entirely hyaline. Calyptrae white with white fringes. Halteres pale yellow. *Legs:* entirely yellow except for mid and hind coxae which are reddish or blackish with grey pollinosity. Fore tibia with the *pv* seta as long as, or even a little longer than, distance from its insertion to apex of tibia, and with two small *ad* setae. Mid femur with two preapical *p* setae, without an *av* comb of strong spines (cf. *macularis*), the *av* surface beyond the submedian setae with only recumbent hairs like those on the general femoral surface, *pv* surface with a row of rather strong but short, almost spine-like, setae in the apical half, the last four to six setae longer than the others; mid tibia without an *ad* seta, the two *pd* setae one and two times as long as tibial diameter. Hind femur with two long *pv* setae in basal half; hind tibia with a ventral preapical lobe and with three (occasionally four) *pv* setae, the *d* preapical seta short and only about half as long as hind metatarsus; hind tarsus simple. *Abdomen:* similar to *macularis* (Fig. 46), laterally compressed towards the apex, T5 forming a strongly flattened dorsal

keel, lateral lobes of sternite 5 large and subtriangular. T1 + 2 and T3 reddish-yellow, T3 occasionally with an indistinct median dorsal orange-brown or red-brown mark; T4 reddish-yellow laterally and pale yellowish along postero-dorsal margin, with dark reddish or blackish-brown median and sublateral spots separated by broad pale grey pollinose areas, the sublateral spots merging gradually into the reddish-yellow colour of the sides of the tergite and not delimited externally by grey pollinose areas; T5 blackish or reddish-black in ground colour with dense pale yellowish-grey pollinosity, without spots or with only a minute trace of sublateral spots, dorsal keel dark brownish; T7 + 8 dark red-brown or blackish in ground colour with pale yellowish-grey pollinosity. Venter, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. T5 with very long backwardly-directed setae on the dorsal keel, the setae distinctly flattened, and with numerous slightly flattened and slightly upcurved setae laterally, ventro-apical margin with numerous very long setae one or two of which are longer than the others; T7 + 8 with numerous outstanding setae similar to those on T5. Hypopygium as in Fig. 79, paralobes large and broad, each with a dense inwardly-directed fringe of hairs on the middle part of posterior margin. *Measurements*: body length 6.0 mm (range 5.8 to 6.2 mm), wing length 5.2 mm (range 5.1 to 5.3 mm) [7 specimens].

♀. Not certainly known, but probably with partially dark brown femora and sublateral spots of T3 and T4 not reaching sides of tergite; presumably without ♂ secondary characters (tibial lobe, *pv* setae on hind tibia, elongate antennae, comb of *pv* setae on mid femur).

Affinities

A species which is very closely allied to *P. macularis* (Wiedemann), but distinguished by the absence of an *av* comb of spines on the mid femur and by the presence of 3-4 (instead of one) *pv* setae on the hind tibia. It would not be unreasonable to regard it only as a subspecies of *macularis* (especially since the ♂ hypopygium is almost indistinguishable) but the two are not allopatric, and for the present it is best to consider *maculipennis* and *macularis* as distinct species.

Material examined

Lectotype ♂, KRAKATAU ISLANDS: v.1908 (*E. Jacobson*) and paralectotype ♂ with same data. CELEBES: 2 ♂♂, Minahassa, 27.vi.1954 (*A.H. G. Alston*) (B.M.Nat. Hist.). FORMOSA: 1 ♂, Takao, 29.iii.1907 (*H. Sauter*) (B.M.Nat.Hist.); 1 ♂, Lambeh, ii.1908 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 1 ♂, Koshun, i.1909 (*H. Sauter*) (D.Ent.Inst.); 3 ♂♂, Koshun, i.1909 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 2 ♂♂, Kankau (Koshun), 7.vii. and 7.xi.1912 (*H. Sauter*) (U.S.Nat.Mus. and D.Ent.Inst.); 1 ♂, Paroe, N. Paiwan District, 7.ix.1912 (*H. Sauter*) (D.Ent.Inst.).

In addition to the ♂ specimens listed above I have seen one ♀ which I believe is probably the ♀ of *maculipennis* although definite association cannot be made. The data of this specimen are: FORMOSA: Kankau (Koshun), 7.ix.1912 (*H. Sauter*) (U.S.Nat.Mus.). It will be noticed that this ♀ has almost identical data with two of the ♂ *maculipennis* collected by Sauter and listed above, so that its association with *maculipennis* is probably correct.

Distribution

Formosa and Indonesia only so far as is known, the type locality being Krakatau Islands in the strait between Sumatra and Java. Literature references to *P. maculipennis* Stein in Krakatau are given by de Meijere (1910) and Dammerman (1922) who record the type material as from Verlaten Island and Lang Island in the Krakatau group. Dammerman (1948) records the species from Anak Krakatau, in 1933. Hennig (1941) also records it from Krakatau (record based on type material).

Pygophora confusa Stein, 1915

Pygophora confusa Stein, 1915, *Suppl. ent. Berl.* 4: 54. Lectotype ♂, FORMOSA. In the Deutsches Entomologisches Institut, Berlin.

Lectotype designation: *P. confusa* was described from four ♂ syntypes. One of these syntypes in the Deutsches Entomologisches Institut has been selected and labelled as lectotype. The syntype originally in the Budapest Museum was destroyed in 1956.

Diagnosis

Mid tibia with a submedian *ad* seta, ♂ hind tibia with a preapical lobe; femora of ♀ yellow and third antennal segment largely brown.

Description

♂. *Head:* occiput pale grey pollinose. Interfrontal area brownish-yellow or orange-yellow. Face and parafacials yellowish-white pollinose. Ocellar setae short and fine, about equal in length to upper reclinate frontal setae but finer. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellow-orange basally but brownish on third segment, the third segment rather short, about 2.5 times as long as second segment and falling short of mouth-margin by about two-thirds of its length; arista long-plumose on basal two-fifths. Palpi pale yellow. Mentum yellowish-brown. *Thorax:* ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; with some pale yellowish-brown pollinosity and with traces of brownish *dc* vittae, scutellum evenly grey pollinose. Presutural acrostichal hairs in two close-set rows; the *dc* setula preceding *prst dc* seta indistinct; two *post ia* setae present but the anterior one short and fine and but slightly differentiated from the *ia* hairs. *Wings:* entirely hyaline, without trace of dark apical suffusion. Calyptrae white with white fringes. Halteres yellow. *Legs:* entirely yellow except for mid and hind coxae which are partly reddish with grey pollinosity. Fore tibia with the *pv* seta short and fine, only about two-thirds as long as the distance from its insertion to apex of tibia, and with two small *ad* setae. Mid femur with two preapical *p* setae, without specialised bristling on either *av* or *pv* surfaces; mid tibia with a small submedian *ad* seta, the two *pd* setae about one and a half and two times as long as the tibial diameter. Hind femur on *pv* surface with two long submedian setae and a smaller seta nearer the base; hind tibia with a ventral preapical lobe and a single submedian *pv* seta, the *d* preapical seta almost as long as hind metatarsus; hind tarsus

simple. *Abdomen* (Fig. 44): laterally compressed towards the apex, T5 forming a subconical dorsal prominence, lateral lobes of sternite 5 large and rounded. T1 + 2 and T3 yellow with only a reddish-brown median dorsal mark on T3; T4 yellow laterally and with well marked reddish-brown median and sublateral spots surrounded by silvery-grey pollinosity, apical margin narrowly yellowish; T5 reddish-yellow ventro-laterally and brown dorsally with pale grey pollinosity and a trace of small brown sublateral spots; T7 + 8 dark reddish with pale grey pollinosity. Venter, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. T5 dorsally with very long outstanding slightly flattened setae and dorso-laterally with long upcurved setae, laterally with an area of short strong upwardly-directed spinous setae, ventro-apical margin with a row of long rather fine setae; T7 + 8 with long, curved slightly flattened setae similar to those on T5. Hypopygium as in Fig. 81 each paralobe with a dense fringe of inwardly-directed hairs on the posterior margin. *Measurements*: body length 5.4 mm (range 5.3 to 5.5 mm), wing length 4.8 mm (range 4.7 to 4.9 mm) [13 specimens].

♀. Generally similar to ♂ with all yellow femora. Abdomen with T1 + 2 slightly darkened medially; T3 and T4 with large well marked blackish-brown median and sublateral spots, and also with a blackish-brown ventro-lateral spot on either side; T5 with a trace of a median longitudinal yellowish-brown line and with blackish-brown sublateral and ventro-lateral spots. T4 without median discal setae, T5 with a pair of strong median discal setae in addition to the pair of discal setae standing on the sublateral spots. Hind femur with three long subequal *pv* setae in the basal three-fifths; hind tibia without preapical lobe. *Measurements*: body length 6.0 mm, wing length 5.4 mm [1 specimen].

Affinities

This is a curious species, as Stein's name suggests, since it is closely similar to *P. immaculipennis* Frey (both species having an *ad* seta on the mid tibia and females with all yellow femora) but in *P. confusa* there is a preapical lobe on the hind tibia of the male as in *P. respondens* and its allies. The male hypopygium is very like that of *immaculipennis* and also closely similar to that in *P. macularis* (Wiedemann)—cf. Figs. 80, 81 and 84.

Material examined

Lectotype ♂, FORMOSA: Tainan, ii.1909 (*H. Sauter*); paralectotype ♂, FORMOSA: Tainan, iii.1909 (*H. Sauter*) (D.Ent.Inst.). FORMOSA: 1 ♂, Takao, 19.vii.1907 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 1 ♂, Takao, 20.viii.1907 (*H. Sauter*) (U.S.Nat. Mus.); 1 ♀, Hokuto, xii.1912 (*H. Sauter*) (U.S.Nat.Mus.); CHINA: 1 ♂, Szechwan, Suifu (Ipin), 10.x.1930 (*D. C. Graham*) (B.M.Nat.Hist.).

Distribution

Formosa and Southern China. In addition to the above Formosan localities it has been recorded from Yentempo by Stein (1915) in his original description, but the syntype from this locality was in Budapest and has been destroyed. Stein (1920a) has recorded *P. confusa* from Labuan Badjan, Simeulue Island (= Simalur), Sumatra, but I have not seen the single male specimen on which the record was

based; it is possible that the record refers to *P. torrida* (Wiedemann) which is known from other Sumatran material and in which there is also an antero-dorsal seta on the mid tibia.

Pygophora torrida (Wiedemann, 1830)

Coenosia torrida Wiedemann, 1830, *Auss. Zweifl. Ins.* 2: 437. Holotype ♀, SUMATRA. In the Universitetets Zoologiske Museum, Copenhagen.

Atomogaster triseriata Walker, 1862, *J. Proc. Linn. Soc.* 6: 11. Holotype ♀, GILOLO (= Halmahera Island, Indonesia). In the British Museum (Natural History), London. **Syn. n.**

Coenosia compressicauda Stein, 1900, *Ann. Mus. Stor. nat. Genova* (2) 20: 391. Holotype ♂, CELEBES. In the Museo Civico di Storia Naturale, Genoa.

Diagnosis

♂. Without a preapical lobe on hind tibia, with an *ad* seta on mid tibia *and* with sublateral spots of T5 large and well developed. ♀ with dark femora *and* an *ad* seta on mid tibia.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area deep orange or brownish-orange. Face and parafacials silvery-white pollinose. Ocellar setae very fine and shorter than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae with first two segments pale orange-yellow, third segment pale yellow with heavy white pollinosity and about 2.8 to 3.0 times as long as second segment, falling short of mouth-margin by about two-fifths of its length; arista long-plumose on basal two-fifths. Palpi yellowish-white. Mentum red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae, mesonotum and scutellum all pale grey pollinose, the pollinosity thin on pleurae, mesonotum without trace of vittae. Presutural acrostichal hairs in two rows; no *dc* setula distinguishable in front of *prst dc* seta; only one distinct *post ia* seta present, the preceding *ia* hair-like. *Wings*: entirely hyaline, without trace of preapical dark suffusion. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for mid and hind coxae which are reddish or blackish with grey pollinosity. Fore tibia with the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia, and with two *ad* setae. Mid femur with two preapical *p* setae, without specialised *av* or *pv* setulae; mid tibia with a well-developed submedian *ad* seta, the two *pd* setae two and three times as long as tibial diameter. Hind femur with two very long widely spaced *pv* setae, the second one distinctly in the apical half; hind tibia without preapical lobe, with one small *pv* seta in basal half, the *d* preapical seta almost as long as hind metatarsus, other setae also very long; hind tarsus simple. *Abdomen* (Fig. 56): slightly laterally compressed towards the apex, T5 in lateral view higher than T7 + 8 but not forming a strongly flattened keel, lateral lobes of sternite 5 large and evenly curved on posterior margin. T1 + 2 and T3 reddish-yellow or pale reddish-orange with traces of white pollinosity basally and apically, T3 with an indistinct

median dorsal red-brown mark; T4 largely darkish, only reddish ventro-laterally, with large dark reddish-brown or blackish-brown median and sublateral spots separated by silvery-grey pollinose areas, areas outside the sublateral spots also thinly silvery pollinose; T5 blackish in ground colour, thinly silvery-grey pollinose except on the black-brown or black median and sublateral spots, the sublateral spots rather large and distinct and each nearly equal in width to silvery-grey pollinose area between median and sublateral spot; T7 + 8 black in ground colour, mainly pale grey pollinose but with some yellowish-brown thin pollinosity dorso-apically. Venter, lobes of sternite 5 and paralobes of hypopygium reddish. T5 with six strong dorsal marginal setae, the median two standing close together on prominent dorsal part of tergite, ventro-apical margin with usual row of strong setae; T7 + 8 with moderately strong dorsal marginal setae, the dorso-lateral setae below these only weakly developed and inconspicuous in dorsal view. Hypopygium as in Fig. 83, paralobes broad, posterior margins with inwardly-directed fringes of spinous setae, inner surface of each near apex with an area of short spinules. *Measurements*: body length 5.3 mm (range 5.1 to 5.4 mm), wing length 4.7 mm (range 4.4 to 4.9 mm) [3 specimens].

♀. All femora blackish-brown on basal four-fifths, only apices yellow. Abdomen with T1 + 2 yellow or reddish-yellow, sometimes with a brownish dorsal mark; T3 and T4 largely dark reddish-brown or blackish-brown, the dark colour separated by longitudinal dorsal pale grey pollinose areas into a median spot and sublateral "spots", the latter extending round to the ventral surface so that most of the tergite is dark, only ventral extremities and apical margins narrowly yellowish; T5 dark red-brown or blackish-brown laterally, yellowish-grey pollinose in median dorsal area and grey pollinose ventro-apically. T4 without median discal setae but marginal setae very strong, T5 with very strong discal setae including a pair of median discs standing on the median pollinose area. Hind femur with three long *pv* setae; hind tibia without *pv* seta. Mesonotum with distinct traces of yellowish-brown pollinose *dc* vittae and sometimes similar traces of an *acr* vitta. Two distinct *post ia* setae. *Measurements*: body length 5.6 mm (range 5.2 to 5.9 mm), wing length 4.8 mm (range 4.4 to 5.1 mm) [6 specimens].

Affinities

P. torrida is very closely related to *P. immaculipennis* Frey, both species possessing an *ad* seta near the middle of the mid tibia and both differing from *P. confusa* Stein (which also has a submedian *ad* seta on this tibia) by the absence of a preapical lobe on the ♂ hind tibia. The ♀ of *torrida* is easily distinguished from the ♀ of *immaculipennis* by the dark femora, but the males of the two species are very closely alike and easily confused; *P. torrida* ♂ can however be distinguished by the large sublateral spots of T5 and by the weaker abdominal bristling. The shape of the paralobes of the hypopygium is also very slightly different.

Material examined

Coenosia torrida Wiedemann, holotype ♀, SUMATRA (no other data). *Atomogaster triseriata* Walker, holotype ♀, GILOLO [= Halmahera Island, Indonesia] (no other

data). *Coenosia compressicauda* Stein, holotype ♂, CELEBES: Kandari, iv.1874 (*O. Beccari*). SUMATRA: 1 ♀, Sungei Penok, Korinchi Valley, 12.iii.1914 (—) (B.M.Nat.Hist.); 1 ♂, 2 ♀♀, Fort de Kock, 1925 (*E. Jacobson*) (U.S.Nat.Mus.). JAVA: 1 ♂, Pekalongan, iv.1907 (*F.M.*) (B.M.Nat.Hist.); 1 ♀, Pekalongan, iv.1907 (*F.M.*) (Bishop Mus.); 1 ♂, 1 ♀, Pekalongan, — (*F. Muir*) (B.M.Nat.Hist.); 1 ♂, Djoeja, vi.1907 (*F. Muir*) (Bishop Mus.); 3 ♂♂, 1 ♀, Buitenzorg, — (*F. Muir*) (Bishop Mus.); 1 ♀, —, xi.1907 (—) (Bishop Mus.); 2 ♀♀, —, — (—) (U.S.Nat.Mus.). PHILIPPINE ISLANDS: 1 ♂, Port Bauge, i.1915 (—) (B.M.Nat.Hist.); 1 ♀, Port Bauge, i.1915 (—) (U.S.Nat.Mus.); 1 ♂, 1 ♀, Los Banos, — (*P. I. Baker*) (U.S.Nat.Mus.); 1 ♀, Luzon, Limay, 21.x.1913 (*G. Boettcher*) (U.S.Nat.Mus.).

Distribution

Only so far as is known from Indonesia and the Philippines. I have seen no material from Formosa, where the very closely related species *P. immaculipennis* is common (the Formosan records given by Hennig (1941) all relate to *immaculipennis* Frey and not *torrida* Wiedemann). The specimen cited above from Sungei Penok, Sumatra, was mentioned by Malloch (1922, p. 383), but the specimen doubtfully assigned to this species (from Siam) belongs to *P. respondens* (Walker); as Malloch pointed out, it lacks the submedian *ad* seta of the mid tibia.

Pygophora immaculipennis Frey, 1917

Pygophora immaculipennis Frey, 1917, *Öfvers. finska VetenskSoc. Forh.* 59: 15. Lectotype ♂, CEYLON. In the Museum Zoologicum Universitatis, Helsinki.

Lectotype designation: *P. immaculipennis* was described from a ♂ and a ♀ syntype (both in Helsinki). The ♂ syntype has been selected and labelled as lectotype and the ♀ syntype labelled as paralectotype.

Diagnosis

Mid tibia with a submedian *ad* seta, ♂ hind tibia without a preapical lobe and sublateral spots of T5 very small (narrower than the pollinose area between a sublateral spot and median spot); ♀ with yellow femora as in ♂ (cf. *P. torrida* (Wiedemann)) and third antennal segment not definitely brown in apical two-thirds.

Description

♂. *Head:* occiput pale grey pollinose. Interfrontal area deep yellow or orange-yellow, sometimes slightly reddish posteriorly. Face, parafacials and parafrontals pale yellowish-white pollinose. Ocellar setae small, shorter and finer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae with first two segments pale orange-yellow and third segment pale yellow but densely white pollinose, third segment about 3.25 times as long as second segment and falling short of mouth-margin by about two-fifths of its length; arista long-plumose on basal two-fifths. Palpi yellowish-white. Mentum reddish-brown. *Thorax:* ground colour entirely blackish,

humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely yellowish-grey pollinose, mesonotum pale yellow or yellowish-grey pollinose but more grey at the edges and without vittae. Presutural acrostichal hairs in two rows; no *dc* setula differentiated in front of *prst dc* seta; two *post ia* setae usually clearly differentiated but anterior one sometimes weak and hair-like. *Wings*: entirely hyaline, without trace of a preapical dark mark. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for mid and hind coxae which are reddish or reddish-black with pale grey pollinosity. Fore tibia with two *ad* setae, the *pv* seta only a little over half as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, without specialised bristling, with three very long *pv* setae and a smaller *pv* seta near the base; mid tibia with a well developed submedian *ad* seta, the two *pd* setae about two and three times as long as tibial diameter. Hind femur with two very long widely spaced *pv* setae and a much smaller *pv* seta near the base; hind tibia without a preapical lobe, with a single well developed *pv* seta in the basal half, the *d* preapical seta almost as long as hind metatarsus and the other setae of extensor surface also long; hind tarsus simple. *Abdomen* (Fig. 55): slightly laterally compressed towards the apex, T5 in lateral view higher than T7 + 8 but not forming a strongly flattened keel, although it is slightly prominent, lateral lobes of sternite 5 large. T1 + 2 and T3 pale reddish-yellow with traces of white pollinosity basally and apically, T3 sometimes with an indefinite or a well-developed median reddish-brown mark; T4 mainly dark in ground colour but reddish-yellow ventro-laterally and along the hind margin, with large boldly marked blackish-brown or dark red-brown median and sublateral spots separated by yellowish-grey pollinose areas, areas immediately outside the sublateral spots also yellowish-grey pollinose; T5 mainly dark brown or blackish in ground colour with a large triangular black-brown spot on the prominent median dorsal part of the tergite and a pair of small blackish sublateral spots which are usually narrow and elongate and not nearly as wide as the pollinose areas between the sublateral spots and the median spot, areas between the spots and sides of the tergite densely greyish-yellow pollinose; T7 + 8 blackish in ground colour with pale yellowish or yellowish-grey pollinosity, without spots; epandrium dark reddish-brown with greyish pollinosity. Venter, lobes of sternite 5, and paralobes of hypopygium reddish-yellow. T5 with six long strong backwardly-directed dorsal marginal setae, the ventro-apical marginal setae of T5 somewhat irregular; T7 + 8 with strong dorsal marginal setae and the dorso-lateral setae (just below the very strong setae) also moderately strong. Hypopygium as in Fig. 84, paralobes large and broad, each with an inwardly-directed fringe of bristly hairs on the posterior margin and an area of dense small hairs near the apex on the inner surface. *Measurements*: body length 5.2 mm (range 4.8 to 5.6 mm), wing length 4.8 mm (range 4.3 to 5.3 mm) [29 specimens].

♀. Femora yellow as in ♂, hind tibia without a *pv* seta. Abdomen with T1 + 2 yellow or pale reddish-yellow, sometimes with an indefinite reddish-brown median mark; T3 reddish-yellow ventro-laterally and narrowly along the margins dorsally, with well marked dark red-brown or blackish-brown median and sublateral spots which are separated by pale yellowish-grey pollinose areas, areas outside the sublateral spots also pale yellowish-grey pollinose; T4 mainly dark in ground colour,

only pale reddish-yellow along the hind margin, with very large bold nearly black median and sublateral spots (the latter often more or less continuing around the sides of the tergite to the ventral surface) separated by densely yellow-grey pollinose areas; T5 dark in ground colour with yellowish-grey pollinosity and a pair of large blackish sublateral spots and a pair of ventro-lateral spots, without a median spot but the tergite distinctly yellowish-brown pollinose in the median line. T4 without median discal setae, T5 with a pair of strong erect median discal setae in addition to the pair of discal setae standing on the sublateral spots. Measurements: body length 5.6 mm (range 5.0 to 5.9 mm), wing length 5.0 mm (range 4.5 to 5.4 mm) [30 specimens].

Affinities

Very closely allied to *P. torrida* (Wiedemann), both species having a submedian *ad* seta on the mid tibia and lacking a preapical lobe on the ♂ hind tibia (the latter distinguishes *P. immaculipennis* and *P. torrida* from *P. confusa* Stein in which this lobe is present). The ♀ of *immaculipennis* is easily distinguished from *torrida* by having all yellow femora, but the ♂ is extremely similar to the *torrida* ♂ and the two can easily be confused; in *immaculipennis* ♂ however the sublateral spots of T5 are very small and much narrower than the pollinose areas between them and the median spot and there are slight differences in the shape of the paralobes.

Material examined

Lectotype ♂, CEYLON: Anuradhapura, 19–21. xii.1910 (*A. Luther*). Paralectotype ♀, data as for lectotype. CEYLON: 1 ♂, Pankullam, 1.i.1891 (*Yerbury*) (B.M. Nat.Hist.); 1 ♂, Mahintalli, 12.xii.1890 (*Yerbury*) (B.M. Nat.Hist.); 1 ♂, Trincomali, 18.xii.1890 (*Yerbury*) (B.M. Nat.Hist.); 1 ♂, Mahaganay, 30.xi.1890 (*Yerbury*) (B.M. Nat.Hist.); 1 ♂, Suduganga, 26.v.1919 (—) (B.M. Nat.Hist.); 2 ♂♂, Hingurakgoda, 20.xii.1953 (*F. Keiser*) (B.M. Nat.Hist.); 1 ♂, Welimada, Uva Ben Head, 24.ix.1953 (*F. Keiser*) (B.M. Nat.Hist.); 1 ♀, Welimada, Uva Ben Head, 24.ix.1953 (*F. Keiser*) (Nat. Mus. Basel); 1 ♂, Kandy, 29.x.1953 (*F. Keiser*) (B.M. Nat.Hist.); 1 ♀, Kandy, 29.x.1953 (*F. Keiser*) (Nat. Mus. Basel); 1 ♀, Kandy, L. Blake's Drive, 11.vi.1953 (*F. Keiser*) (B.M. Nat.Hist.); 1 ♀, Belihul Oya, 11.ii.1954 (*F. Keiser*) (B.M. Nat.Hist.); 1 ♀, Peradeniya, Exper. Stat., 5.vi.1953 (*F. Keiser*) (B.M. Nat.Hist.); 1 ♂, Haragama, 14.i.1954 (*F. Keiser*) (Nat. Mus. Basel); 1 ♂, 1 ♀, Maha Oya, 26.ix.1953 (*F. Keiser*) (Nat. Mus. Basel); 1 ♀, Kalpitiya, 24.i.1954 (*F. Keiser*) (Nat. Mus. Basel); 1 ♀, Ambacotta, 14.xii.1953 (*F. Keiser*) (Nat. Mus. Basel). INDIA: 1 ♀, Bihar, Banhar, 25.ix.1921 (*H.A.I.*) (B.M. Nat.Hist.); 1 ♀, Bihar, Pusa, 13.xi.1920 (—) (B.M. Nat.Hist.); 1 ♀, Assam, 10 mls. N. of Tinsukla, 29.ii.1944 (*D. E. Hardy*) (U.S. Nat. Mus.). BURMA: 1 ♀, Rangoon, 8.vi.1918 (—) (B.M. Nat.Hist.). CHINA: 1 ♂, Foochow, 1936–37 (*M. S. Yang*) (B.M. Nat.Hist.); 1 ♂, Lo Fou Shan, 1906 (*F. Muir*) (B.M. Nat.Hist.). HONG KONG: 5 ♀♀, Hong Kong, 4–5. iii.1906 (*Brunetti*) (B.M. Nat.Hist. and Zool. Mus. Humb. Univ.). MACAO: 1 ♂, Macao, i.1907 (*F. Muir*) (Bishop Mus.). FORMOSA: 4 ♂♂, 2 ♀♀, Chip-Chip, ii–iii.1909 (*H. Sauter*) (D. Ent. Inst. and Zool. Mus. Humb. Univ.); 1 ♀, Chosokei, 1914 (*H. Sauter*) (D. Ent. Inst.); 1 ♀, Daitotei, v–vi.1914 (*H. Sauter*) (D. Ent. Inst.); 1 ♂, Gyamma, vi.1907

(*H. Sauter*) (Zool.Mus.Humb.Univ.); 3 ♂♂, Hokuto, xii.1912 (*H. Sauter*) (U.S. Nat.Mus. and D.Ent.Inst.); 1 ♂, Hoozan, 1911 (*H. Sauter*) (D.Ent.Inst.); 1 ♀, Kagi, 10.viii.1907 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 2 ♂♂, 1 ♀, Kankau, ix.1912 (*H. Sauter*) (D.Ent.Inst.); 2 ♂♂, Kosempo, 20 and 24.i.1908 (*H. Sauter*) (Zool.Mus. Humb.Univ.); 1 ♀, Koshun, i.1909 (*H. Sauter*) (D.Ent.Inst.); 2 ♂♂, Lambeh, i.1908 (*H. Sauter*) (U.S.Nat.Mus. and Zool.Mus.Humb.Univ.); 1 ♂, Macuyama, v-vi.1914 (*H. Sauter*) (U.S.Nat.Mus.); 1 ♂, 7 ♀♀, Tainan, ii.1909 (*H. Sauter*) (D.Ent. Inst.); 1 ♀, Tainan, ii.1909 (*H. Sauter*) (U.S.Nat.Mus.); 1 ♂, 1 ♀, Taihoku, 7.xi.1912 (*H. Sauter*) (D.Ent.Inst.); 2 ♀♀, Taihoku, 1912 (*H. Sauter*) (B.M.Nat.Hist.); 6 ♂♂, 11 ♀♀, Takao, 29.iii.-7.viii.1907 and 9.i.1908 (*H. Sauter*) (Zool.Mus.Humb.Univ.); 1 ♀, Yentempo, 22.v.1907 (*H. Sauter*) (Zool.Mus.Humb.Univ.). RYUKYU ISLANDS: 1 ♀, Ishigaki I., 1-5.i.1953 (*G. E. Bohart*) (Bishop Mus.).

Distribution

Widespread and probably common in the Oriental region from Ceylon to Formosa and Ryukyu Islands. *P. immaculipennis* appears not to spread into Malaya and Indonesia where its place is taken by the very closely allied species, *P. torrida* (Wiedemann). The four ♂ specimens from Ceylon collected by Lt.-Col. Yerbury and listed above are those mentioned by Malloch (1922, p. 383). Although Malloch correctly recognised *P. immaculipennis* in this paper, he mistook it in a later paper (Malloch, 1929a): he keys out "*immaculipennis*" in the later paper, but this is in error for *macularis* (Wiedemann) and what he calls *macularis* Wied. is really *torrida* Wiedemann. Stein also did not properly recognise *P. immaculipennis*, and considered the Formosa material listed above to belong to *P. macularis* (Wied.) which he wrongly took to be synonymous with *P. torrida* (Wied.); Hennig (1941), following Stein, has listed the Formosan material as *P. torrida*, but the Formosan specimens referred to as *macularis* or *torrida* by Stein and Hennig are misidentified and are *immaculipennis* Frey.

Pygophora apicalis Schiner, 1868

Pygophora apicalis Schiner, 1868, *Nov. Reise, Dipt.*: 295. Lectotype ♂, AUSTRALIA. In the Naturhistorisches Museum, Vienna.

Hoplogaster notatus Bigot, 1884, *Ann. Soc. ent. Fr.* (6) 4: 281. Lectotype ♂, AUSTRALIA. In the British Museum (Natural History), London. First synonymised by Stein, 1907, *Z. Hym. Dipt.* 4: 281.

Pygophora australis Malloch, 1922, *Ann. Mag. nat. Hist.* (9) 10: 383. Holotype ♂, AUSTRALIA. In the British Museum (Natural History), London. **Syn. n.**

Lectotype designations: *P. apicalis* Schiner was described from two ♂ syntypes; one of these has been selected and labelled as lectotype. *H. notatus* Bigot was also described from two ♂ syntypes, of which one has been selected and labelled as lectotype and the other labelled as paralectotype.

Diagnosis

♂. Hind tibia with preapical lobe which ends in strong tooth-like serrations and with a series of seven or eight down-curved *pv* setae in the apical half (Fig. 14).

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area yellowish-orange. Face, parafacials and parafrontals pale yellow pollinose. Ocellar setae well developed, about equal in size to upper reclinate frontal setae or a little longer. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright yellow-orange, third segment about 3.8 times as long as second segment and falling short of mouth-margin by about one-third of its length; arista long-plumose on basal two-fifths. Palpi pale yellowish-white. Mentum dark red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, mesonotum and scutellum pale yellowish-grey pollinose, mesonotum without trace of darker vittae. Presutural acrostichal hairs in two rows, the hairs strong and forming two pairs of small setulae; the *prst dc* seta preceded by a distinct *dc* setula; two distinct *post ia* setae present. *Wings*: usually with a dark preapical spot or suffusion on the end of R_{2+3} , the brownish colour usually extending posteriorly to R_{4+5} or a little beyond, wings sometimes entirely hyaline. Calyptrae white with white fringes. Halteres yellow. *Legs*: entirely yellow except for mid and hind coxae which are reddish with grey pollinosity. Fore tibia with two *ad* setae and some smaller *ad* setulae, the *pv* seta about equal in length to distance from its insertion to the apex of the tibia. Mid femur with two preapical *p* setae, with about six long *av* setae in basal three-fifths, and a sparse row of long *pv* setae which ends in a series of about six short bristly hairs; mid tibia without an *ad* seta, the two *pd* setae short and only about one and one and a half times as long as tibial diameter. Hind femur with only one very long submedian *pv* seta with a smaller seta just beyond it which is only half its length; hind tibia with a ventral preapical lobe which ends in about seven strong tooth-like serrations (Fig. 14) and with a row of seven or eight down-curved *pv* setae in the apical half, the *d* preapical seta short and only about two-thirds as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 43): laterally compressed towards the apex, T5 forming a strongly flattened dorsal keel, lateral lobes of sternite 5 very large. T1 + 2 and T3 yellowish-orange, T3 with a bold median dorsal red-brown or almost black spot; T4 yellowish-orange laterally, with bold dark brown or nearly black median and sublateral spots separated by grey pollinose areas, extreme dorsal apical margin narrowly yellowish; T5 dark brownish or blackish in ground colour and grey pollinose, with small sublateral spots and dorsal keel dark brown or almost black, posterior margin narrowly yellowish laterally; T7 + 8 dark brownish in ground colour with grey pollinosity. Venter and lobes of sternite 5 reddish-yellow, paralobes of hypopygium dark reddish. Bristly hairs of T1 + 2—T4 rather long and erect; T5 with long backwardly-directed flattened setae on the dorsal keel and with very numerous fine upcurved hairs laterally, ventro-apical margin with rather dense tuft of setae; T7 + 8 with long backwardly-directed setae on posterior margin and with fine upcurved hairs similar to those on T5 antero-laterally and dorsally. Hypopygium as in Fig. 85, paralobes strongly clavate and bearing dense tufts of hair on inner postero-apical margins, mesolobes long and strongly curved, bare. *Measurements*: body length 5.56 mm (range 5.4 to 5.8 mm), wing length 5.84 mm (range 5.6 to 6.0 mm) [8 specimens]; wing length con-

sistently longer than body length in all specimens seen, as abdomen unusually contracted.

♀. Femora yellow as in ♂, but wing without preapical dark mark. Abdomen with T1 + 2 pale yellow; T3 largely reddish-yellow laterally but slightly greyish in middle of the sides, dorsally with large brown or blackish-brown median and sublateral spots surrounded by grey pollinose areas, posterior dorsal margin yellowish; T4 reddish-yellow along posterior margin, otherwise darkish in ground colour with yellowish-grey pollinosity except on the large dark brown or black-brown median and sublateral spots; T5 dark in ground colour with pale yellow-grey pollinosity and distinct blackish sublateral spots, median dorsal area with reddish pollinosity. T4 and T5 with slight traces of ventro-lateral spots. T4 without median discal setae, T5 sometimes with a weak pair of median discal setae in addition to the discal setae standing on the sublateral spots. Hind femur with three long *pv* setae as usual in this sex; hind tibia without preapical lobe or *pv* setae. Mesonotum more yellowish than in ♂, and with traces of vittae. Measurements: body length 6.25 mm (range 6.1 to 6.5 mm), wing length 6.1 mm (range 5.9 to 6.3 mm) [11 specimens].

Affinities

A distinctive species with a preapical hind tibial lobe in ♂ but probably not closely allied to other species in which the lobe is present. The affinities are probably most closely with *P. maculigera* (Stein). The ♀ is closely like the ♀ of *P. maculigera* but can be distinguished by the row of strong erect marginal setae on T4 (in *maculigera* ♀ there is only a strong erect median pair of marginal setae on T4, the other marginals being hair-like and recumbent).

Material examined

Pygophora apicalis Schiner, lectotype ♂, AUSTRALIA: Sydney (no other data). *Hoplogaster notatus* Bigot, lectotype and paralectotype ♂, AUSTRALIA (no other data) (B.M.Nat.Hist.). *Pygophora australis* Malloch, holotype ♂, AUSTRALIA: Queensland, Burpengarry, — (T. L. Bancroft). AUSTRALIA: 2 ♂♂, 2 ♀♀, Queensland, Tambourine Mts., 11–26.iv.1935 (R. E. Turner) (B.M.Nat.Hist.); 3 ♂♂, 2 ♀♀, Queensland, Tambourine Mts., 1–25.v.1935 (R. E. Turner) (B.M.Nat.Hist.); 1 ♀, Queensland, Mt. Tambourine, x.1924 (A. Musgrave and C. Geissman) (Aust.Mus.); 1 ♀, Queensland, Burpengarry, — (T. L. Bancroft) (B.M.Nat.Hist.); 1 ♀, Queensland, R. Williams, nr. Cutler's Pass, 24.x.1926 (A. Musgrave and T. G. Campbell) (Aust.Mus.); 2 ♀♀, N.S.W., Sydney, Neutral Bay, 22.x.1910 (J. B. Cleland) (B.M.Nat.Hist.); 3 ♀♀, N.S.W., Sydney, Collaroy, 8.ix.1921 (Health Dept.) (S.P.H.T.M.); 1 ♀, N.S.W., Sydney, "home", 29.x.1922 (S.P.H.T.M.); 1 ♂, N.S.W., Sydney, 3.x.1924 (Health Dept.) (S.P.H.T.M.); 2 ♀♀, N.S.W., Sydney, 17.ix.1922 and 28.x.1923 (Health Dept.) (S.P.H.T.M.); 1 ♀, N.S.W., Sydney, — (—) (S.P.H.T.M.); 1 ♀, N.S.W., Sydney, — (S. Daemel) (Zool.Mus.Humb.Univ.); 1 ♂, N.S.W., Sydney, 14.iii.1918 (C. E. Cole) (Nat.Mus.Vict.); 1 ♀, N.S.W., Sydney, 28.viii.1921 (Health Dept.) (Aust.Mus.); 1 ♂, N.S.W., Sydney, — (—) (Aust.Mus.); 1 ♀, N.S.W., Sydney, Oatley, 4.ix.1921 (A. Musgrave) (Aust.Mus.); 1 ♂, N.S.W., Sydney, 2.ii.1931 (Bullmore) (Aust.Mus.); 1 ♂, N.S.W., Sydney, xii.1902

(*Helms*) (Bishop Mus.); 2 ♀♀, N.S.W., E. Dorriggo, Brooklana, i.1929 (*W. Heron*) (Aust.Mus.); 1 ♂, 2 ♀♀, N.S.W., Bondi, — (—) (Aust.Mus.); 1 ♂, N.S.W., Newcastle, 4.x.1925 (—) (Aust.Mus.); 2 ♀♀, N.S.W., Lone Cove, i.vii. and 24.xi.1927 (—) (Aust.Mus.); 1 ♂, N.S.W., Pt. Macquarie, 25.viii.–14.ix.1941 (*H. W. Simmonds*) (Aust.Mus.); 1 ♂, N.S.W., Blue Mts., 10.ii.1915 (*A. Musgrave*) (Aust.Mus.); 1 ♂, N.S.W., Vancluse (?), 1931 (*K. K. Spence*) (Aust.Mus.); 2 ♂♂, N.S.W., Bronte, 7.v.1955 (*D. K. McAlpine*) (Aust.Mus.); 1 ♀, N.S.W., Bronte, 10.iv.1955 (*D. K. McAlpine*) (Aust.Mus.); 1 ♀, N.S.W., Nowra, 1931 (*F. A. Rodway*) (B.M.Nat.Hist.); 1 ♂, 1 ♀, Victoria, — (*C. French*) (B.M.Nat.Hist.); 1 ♂, Western Australia, Yanchep, 32 mls. N. of Perth, 13–23.xi.1935 (*R. E. Turner*) (B.M.Nat.Hist.); 1 ♂, Western Australia, Yanchep, 32 mls. N. of Perth, 29.i.–8.ii.1936 (*R. E. Turner*) (B.M.Nat.Hist.); 1 ♀, Western Australia, Dongarra, 26.ix.–3.x.1935 (*R. E. Turner*) (B.M.Nat.Hist.); 2 ♂♂, Western Australia, Swan River, — (*Helms*) (Bishop Mus.).

Distribution

An Australian species particularly common in New South Wales, but extending also into Western Australia and Queensland. Examination of the holotype of *P. australis* Malloch, which lacks the dark preapical spot on the wings, shows that it is synonymous with *P. apicalis* Schiner; except for the lack of the wing spot there is no distinction whatever, and the unique hind tibia, the bristling of the tergites and hypopygium are identical with those of the lectotype of *apicalis*. Thus no significance can be attached to the presence or absence of the wing spot, and (as in *Pygophora* generally) this character is of no importance. The structure of the laterally compressed keel-like T5 (apparent fourth tergite) is identical in *australis* and *apicalis*, and Paramonov (1961, p. 511) is in error in stating that *apicalis* has a normally built tergite. Contrary to what Paramonov says (*loc. cit.*) most specimens in Australian museums are correctly identified as *apicalis*. Specimens, both with and without the dark mark on the wings, have been seen from Queensland, New South Wales, Victoria and Western Australia, and intermediate stages occur in which there is only a small and faint dark suffusion. In Queensland both *P. apicalis* and *P. maculigera* (Stein) occur; *maculigera* resembles *apicalis* closely but the ♂ lacks the hind tibial lobe and so is easily distinguished. The females of the two species are very alike but can be separated by the bristling of the hind margin of T4 (see differences mentioned under Affinities above).

Pygophora maculigera (Stein, 1920) **comb. n.**

Coenosia maculigera Stein, 1920, *Tijdschr. Ent.* 62 Suppl.: 85. Holotype ♂, SAONEK. In the Zoölogisch Museum, Amsterdam.

Pygophora aliena Malloch, 1922, *Ann. Mag. nat. Hist.* (9) 10: 381. Holotype ♂, QUEENSLAND. In the British Museum (Natural History), London. **Syn. n.**

Pygophora setiventris Malloch, 1929, *Treubia* 7: 394. Holotype ♂, BURU. In the Zoölogisch Museum, Amsterdam. **Syn. n.**

Diagnosis

♂. T5 with prominent dorsal keel *and* hind tibia without a preapical lobe, T4

on each side with one of the marginal setae usually very long and conspicuous, T5 bearing dense bristles on whole ventral margin and T5 and T7 + 8 laterally with abundant outstanding hairs which are slightly flattened and curved upwards, the long apical setae of the dorsal keel of T5 directed strongly downwards as well as backwards, hind tibia with two *pv* setae in apical half.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area deep yellow. Face, parafacials and parafrontals deep golden-yellow pollinose. Ocellar setae very fine but usually about equal in length to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright yellow-orange, third segment about 4.5 times as long as second segment and falling short of mouth-margin by about a quarter of its length; arista long-plumose on basal half. Palpi yellowish-white. Mentum dark red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and most of dorsum densely grey pollinose, mesonotum without vittae but slightly yellowish-grey pollinose. Presutural acrostichal hairs in two rows; no distinct *dc* setula differentiated in front of *prst dc* seta; two well developed *post ia* setae present. *Wings*: entirely hyaline or sometimes with a faint or distinct brown suffusion on the apex of R_{2+3} . Calyptrae white with white fringes. Halteres yellow. *Legs*: entirely yellow except for mid and hind coxae which are reddish or blackish with grey pollinosity. Fore tibia with two well developed *ad* setae, the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, without specialised bristling but the *pv* setae close-set in the apical quarter and ending with very small setulae; mid tibia without an *ad* seta, the two *pd* setae about one or one and a half times as long as tibial diameter. Hind femur with two very long submedian *pv* setae followed by rather numerous and well developed *pv* setae; hind tibia without a preapical lobe but with two strong *pv* setae in apical half, the *d* preapical seta about two-thirds as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 47): strongly laterally compressed towards the apex with T5 produced dorsally into a prominent keel, lateral lobes of sternite 5 large and subtriangular with the outer surface ventrally bearing numerous minute hairs. T1 + 2 and T3 yellowish with paler yellowish-white hind margins, but without spots or darker colouring; T4 mainly yellowish with very pale hind margin but dorsally with a large dark brown or almost black triangular median spot and a pair of less distinct yellow-brown or reddish-brown sublateral spots, the spots more or less contiguous but overlaid in between by thinly greyish-white pollinose areas, the sublateral spots externally not clearly differentiated and their dark colour merging gradually into the yellowish sides of the tergite; T5 mainly dark reddish-brown in ground colour (pale yellowish laterally against the anterior margin and narrowly on the hind margin) with pale grey pollinosity and with a distinct pair of rounded dark brown sublateral spots, the dorsal keel also dark brown; T7 + 8 dark reddish-brown in ground colour with grey pollinosity and without spots. Venter yellowish, lateral lobes of sternite 5 and paralobes of hypopygium slightly reddish-yellow. T4 on either side with one of the marginal setae

usually exceptionally long, stronger than the others and very conspicuous (shown in Fig. 47); T5 with the dorsal keel bearing several very long flattened setae which are always directed strongly downwards as well as backwards, laterally with numerous outstanding hairs which are distinctly flattened and slightly curved upwards, ventrally and ventro-apically with a very dense tuft of long black setae of which those on the extreme ventro-apical edge are much longer than the others and curved upwards; T7 + 8 dorso-laterally with numerous fine outstanding slightly curved hairs similar to those on T5 but finer and less conspicuously flattened, apically with a group of three or four long backwardly-directed setae. Hypopygium as in Fig. 86, paralobes large and fringed on the posterior apices with dense flattened black setulae, each with three small black pegs on the inner surface towards the apex, the extreme apices slightly produced and truncate. *Measurements*: body length 5.3 mm (range 5.2 to 5.4 mm), wing length 4.7 mm (range 4.5 to 4.9 mm) [4 specimens].

♀. Femora yellow as in ♂, wing always entirely hyaline. Abdomen with T1 + 2 and extreme hind margins of other tergites yellowish; T3 and T4 largely dark in ground colour and grey pollinose, each with large bold blackish-brown median and sublateral spots, the median spots parallel-sided and extending from anterior edge to pale hind margins so that together they form a dark median vitta; T5 dark in ground colour with dense grey pollinosity and a pair of large blackish-brown sublateral spots but without a median spot (although the median longitudinal line is darkened by dark yellowish-brown pollinosity). T4 without median discal setae and with only a single median pair of strong erect marginal setae (the other marginal setae hair-like and recumbent); T5 without median discal setae. *Measurements*: body length 5.8 mm, wing length 5.2 mm [1 specimen].

Affinities

P. maculigera is a distinctive and easily recognised species in the ♂ sex in which the curious downwardly-directed setae on the keel of T5 is a constant feature; it is very closely allied to *P. majalis* Paramonov (which may perhaps be only a form of *maculigera*) and to *P. absentiseta* sp. n. (which differs from *maculigera* in the form of bristling on T5 and in lacking the proximal *pd* seta (♂)). *P. maculigera* also shows considerable affinity with *P. apicalis* Schiner, but lacks the hind tibial lobe. The ♀ of *maculigera* is closely similar to the ♀ of *apicalis* but differs in having only a single strong median marginal pair of setae on T4, the other marginals small and hair-like (in *apicalis* there is a transverse row of strong erect marginals on T4).

Material examined

Coenosia maculigera Stein, holotype ♂, DUTCH NEW GUINEA: Saonek [islet off Waigeo Island], 23.i.1910 (*M. de Beaufort*). *Pygophora aliena* Malloch, holotype ♂, AUSTRALIA: Queensland, Kuranda, 1100 ft., 3.v.-20.vi.1913 (*R. E. Turner*). *Pygophora setiventris* Malloch, holotype ♂, INDONESIA: Buru Island, 10.i.1921 (*L. J. Toxopeus*). Paratype ♂ and paratype ♀ (U.S.Nat.Mus.) and paratype ♂ (Bishop Mus.) of *P. aliena* Malloch, AUSTRALIA: N. Queensland, Babinda, — (*J. F. Illingworth*). CELEBES: 1 ♂, Minahassa, 27.vi.1954 (*A. H. G. Alston*) (B.M. Nat.Hist.); 1 ♀, Minahassa, Tomohon, 12.vii.1954 (*A. H. G. Alston*) (B.M.Nat.

Hist.). DUTCH NEW GUINEA: 1 ♂, Kulima, 1400 m., 19–22.ii.1960 (*T. C. Maa*) (Bishop Mus.). N.E. NEW GUINEA: 13 ♂♂, Minj area, 1700 m., 3.vii.1957 (*D. E. Hardy*) (B.M.Nat.Hist. and Bishop Mus.); 18 ♂♂, Okapa, 64 km. S. of Kainantu, 1800 m., 28 and 29.ix.1959 (*T. C. Maa*) (B.M.Nat.Hist. and Bishop Mus.); 13 ♂♂, 12 ♀♀, Sinofi, 30 km. S. of Kainantu, 1590 m., 1–6.x.1959 (*T. C. Maa*) (B.M.Nat.Hist. and Bishop Mus.); 2 ♂♂, 1 ♀, Sinofi, 30 km. S. of Kainantu, 30.ix.1959 (*T. C. Maa*) (Bishop Mus.); 1 ♂, 1 ♀, Miramar, Asaro V., 1800 m., 27.vi.1955 (*J. L. Gressitt*) (Bishop Mus.); 4 ♂♂, Maprik, 150 m., 29.xii.1959 to 17.i.1960 (*T. C. Maa*) (Bishop Mus.); 1 ♂, Nondugl, 1600m., 9.vii.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♂, Madang, 5m., 28.x.1958 (*J. L. Gressitt*) (Bishop Mus.); 1 ♂, Sepalakambang, Salawaket Range, 1920 m., 12.ix.1956 (*E. J. Ford*) (Bishop Mus.); 1 ♂, Finisterre Range, Saidor, Funiyende, 1200 m., 24.ix.1958 (*W. W. Brandt*) (Bishop Mus.); 1 ♂, W. Highlands, Baiyer R., 1150 m., 17.x.1958 (*J. L. Gressitt*) (Bishop Mus.); 2 ♂♂, Tapo (= Tapu), 1650 m., 3 km. N.W. of Kainantu, 22.x.1959 (*T. C. Maa*) (Bishop Mus.). NEW GUINEA (PAPUA): 1 ♂, 1 ♀, S. Highlands, Aiyuro nr. Mendi, 1530 m., 7.x.1958 (*J. L. Gressitt*) (B.M.Nat.Hist. and Bishop Mus.); 8 ♂♂, 6 ♀♀, S. Highlands, Mendi, 1660 m., 6.x.1958 (*J. L. Gressitt*) (B.M.Nat.Hist. and Bishop Mus.); 1 ♂, 1 ♀, S. Highlands, Mendi, 13.x.1958 (*J. L. Gressitt*) (Bishop Mus.); 1 ♂, Kapagere nr. Rigo, 14–19.v.1959 (*C. D. Michener*) (Bishop Mus.); 1 ♂, Laloki, iv.1909 (*F. Muir*) (Bishop Mus.); 5 ♂♂, Goroka, 1550 m., 10.vi.1955 (*J. L. Gressitt*) (Bishop Mus.); 2 ♂♂, Goroka, 1530 m., 30.iv.–3.v.1959 (*C. D. Michener*) (Bishop Mus.). NEW BRITAIN: 1 ♂, Rabaul, Keravat, 10.vii.1924 (*J. L. Froggatt*) (B.M.Nat.Hist.); 1 ♂, Vunabakan, 10 km. E. of Keravat, 180 m., 16–20.xi.1959 (*T. C. Maa*) (Bishop Mus.). SOLOMON ISLANDS: 1 ♂, Bougainville, Simba Mission, 30.vi.1956 (*E. J. Ford*) (Bishop Mus.). AUSTRALIA: 1 ♂, Queensland, Palm Is., — (*M. Taylor*) (U.S.Nat.Mus.); 1 ♀, N. Queensland, Kuranda, 21.vi.–24.vii.1913 (*R. E. Turner*) (B.M.Nat.Hist.).

Distribution

From eastern Indonesia (Celebes) to Solomon Islands, southwards into northern Queensland; apparently abundant in New Guinea. The type locality of *P. maculigera* is Saonek, which is not marked on most maps of Indonesia and New Guinea; Saonek is a village and islet near the southern shore of Waigeo Island near the entrance to the Majalibit inlet, Waigeo itself lying off the north-west tip of the Vogelkop of Dutch New Guinea. The citation of Ceram as the type locality of *maculigera* by Séguy (1937) is erroneous. Hennig (1952) records *P. maculigera* (under the name *aliena* Malloch) from Sembaloen in the island of Lombok (Indonesia); I have not seen the specimen on which the record is based.

Pygophora majalis Paramonov, 1961

Pygophora majalis Paramonov, 1961, *Ann. Mag. nat. Hist.* (13) 3: 509. Holotype ♂, AUSTRALIA. In the Division of Entomology Museum, C.S.I.R.O., Canberra.

Diagnosis

♂. Distinguished by combination of flattened keel to T5, absence of preapical lobe on hind tibia and presence of a dense tuft of strong black bristly hairs apically

on T7 + 8 (Fig. 48). Apex of *p* surface of mid femur with an area of small setulae (Fig. 26).

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area dull yellow. Face yellowish-white pollinose; parafacials pale yellowish pollinose. Ocellar setae equal in length to, but finer than, upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae pale orange-yellow, third segment about 3.6 times as long as second segment and falling short of mouth-margin by about a quarter of its length; arista long-plumose on basal two-fifths. Palpi white. Mentum dark red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, slightly yellowish-grey on mesopleura, mesonotum and scutellum pale yellowish-grey pollinose and with almost no trace of mesonotal vittae. Presutural acrostichal hairs in two rows; the *dc* setula preceding the *prst* *dc* seta very indistinct, smaller than the *acr* hairs; two very well developed *post ia* setae present. *Wings*: entirely hyaline, without trace of apical dark suffusion. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for mid and hind coxae which are largely reddish-black with grey pollinosity. Fore tibia with *pv* seta strong (about equal in length to distance from its insertion to apex of tibia) and with two or three small *ad* setae. Mid femur with two pre-apical *p* setae, with an area of small close-set setulae at apex of *pv* surface, and with long and fine *pv* setae (Fig. 26); mid tibia without an *ad* seta, the two *pd* setae one and two times as long as tibial diameter. Hind femur with a row of six very long strong *pv* setae in the apical half and three or four short *pv* setae in the basal half; hind tibia without a preapical lobe, with one or two small *pv* setae, the *d* preapical seta short and only a little over half as long as hind metatarsus, which is unusually long. *Abdomen* (Fig. 48): laterally compressed towards the apex, T5 forming a strongly flattened dorsal keel, lateral lobes of sternite 5 large and subtriangular. T1 + 2 and T3 yellow, T3 with a very small dark brown median dorsal mark; T4 yellow latero-ventrally and narrowly along the apical margin, with large well marked dark brown median and sublateral spots which are separated by grey pollinose areas; T5 dark in ground colour, densely grey pollinose except on the dark brown dorsal keel and on the pair of well marked dark brown sublateral spots, lateral apical margins indistinctly yellowish. Venter, lobes of sternite 5 and paralobes of hypopygium yellow. T5 with long narrow flattened and backwardly-directed setae on dorsal keel and with numerous up-curved setae laterally, ventro-apical margin with a dense tuft of long, slightly sinuous setae; T7 + 8 with long fine slightly upcurved setae similar to those on the sides of T5, ventro-apically with a characteristic dense matt of long black setae and hairs. Apices of paralobes with short dense curved setulae. *Measurements*: body length 5.3 mm, wing length 5.1 mm [1 specimen].

♀. Unknown, probably closely similar to ♀ of *P. maculigera* (Stein).

Affinities

Closely allied to *P. maculigera* (Stein) but distinguished by the dense tuft of

hairs on T7 + 8 and by the area of small *pv* setulae at the apex of the mid femur. *P. majalis* is generally less bristly than *P. maculigera*, especially on the ventro-apical margins of T5, and there is no long lateral marginal seta on the side of T4 as occurs in *maculigera*.

Material examined

Holotype ♂, AUSTRALIA: New South Wales, Church Point, 13.v.1959 (*I. F. B. Common*).

Distribution

Known only from New South Wales, from the holotype specimen and from one ♂ paratype from Narara, 14.iv.1950 (*A. Dyce*).

Pygophora caledonica (Bigot, 1885)

Coenosia ? caledonica Bigot, 1885, *Ann. Soc. ent. Fr.* 4: 269. Holotype ♀, NEW CALEDONIA. In the British Museum (Natural History), London.

No diagnosis can be given for this species since I have not seen the ♂ and the ♀ possesses no diagnostic characters. However the ♂ can be approximately placed from its possession of a keeled T5 to the abdomen combined with a simple hind tibia, characters mentioned by Paramonov (1961).

Description

♀. *Head*: occiput pale grey pollinose. Interfrontal area yellowish-orange. Face, parafacials and parafrontals yellowish-white pollinose. Ocellar setae well developed, about as long as but finer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae pale yellowish-orange, third segment about 2.8 times as long as second segment and falling short of mouth-margin by about two-fifths of its length; arista long-plumose on basal half. Palpi probably yellowish-white and mentum probably dark brown (both missing in holotype). *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, dorsum yellow-grey pollinose with traces of three darker yellowish-brown pollinose vittae. Presutural acrostichal hairs in two rows; no distinct *dc* setula preceding *prst dc* seta; two *post ia* setae present. *Wings*: hyaline with a very faint yellowish tinge. Calyptrae pale yellowish with yellowish-white fringes. Halteres pale yellow. *Legs*: almost entirely yellow including the fore coxae, mid and hind coxae reddish-brown with pale grey pollinosity. Fore tibia with two or three small *ad* setae. Mid femur with two preapical *p* setae; mid tibia without an *ad* seta. Hind femur with three long *pv* setae in basal two-thirds; hind tibia without *pv* setae. *Abdomen* (missing in holotype) probably reddish basally and perhaps ventrally on posterior half but T4 and T5 and some of T3 dorsally largely dark brown or blackish in ground colour with yellow-grey pollinosity, these three tergites with sublateral dark brown or blackish spots and T3 and T4 also with dark median spots, the three spots perhaps sometimes more or less coalesced on

T4. T4 and T5 without median discal setae. *Measurements*: approximate body length 6.0 mm, approximate wing length 5.5 mm.

♂. Briefly described by Paramonov (1961) but no figures given and ♂ genitalia not examined. Apparently with the following characters: antennae with third segment very elongate and nearly reaching mouth-margin, wing with preapical dark spot on anterior margin (apex of R_{2+3}), mid femur without specialised bristling, hind tibia without a preapical lobe (? with one or two *pv* setae), abdomen strongly laterally compressed towards the apex with T5 forming a prominent flattened dorsal keel, T5 with long dense bristles on ventro-apical areas (presumably as in *P. maculigera*), sternite 5 with medium-sized rounded lobes.

Affinities

From Paramonov's (1961) description of the ♂ it is clear that *P. caledonica* (Bigot) is closely allied to *P. maculigera* (Stein) and to *P. majalis* Paramonov, both of which possess the combination in the ♂ of a simple hind tibia and the strongly keeled T5 of the abdomen.

Material examined

Holotype ♀, NEW CALEDONIA (no other data).

In addition I have seen two females collected by Miss Cheesman in New Hebrides which may belong to this species. Data as follows: NEW HEBRIDES: 1 ♀, Malekula, Ounua, iii-iv.1929 (*L. E. Cheesman*) (B.M.Nat.Hist.) and 1 ♀, Malekula, ii.1930 (*L. E. Cheesman*) (B.M.Nat.Hist.).

Distribution

Only definitely known from New Caledonia but possibly also occurring in New Hebrides. The exact type locality in New Caledonia is not known, but Paramonov (1961) has recorded *P. caledonica* from Noumea, Ause-Vata (13.v.1955, *J. Rageau*).

***Pygophora absentiseta* sp. n.**

Diagnosis

♂. Distinguished from all other *Pygophora* by the absence of the proximal *pd* seta of the hind tibia; ♂ abdomen laterally flattened apically with T5 produced into a prominent dorsal keel and bearing on the sides dense erect setae the uppermost ones of which are lanceolate and downswept (Fig. 50), hind tibia with a very strong *pv* seta slightly hooked at the tip and inserted at about one third from the base followed by a row of smaller *pv* setae which decrease in size distally (Fig. 17).

Description

♂. *Head*: occiput pale grey pollinose, more yellowish towards the eye-margins. Interfrontal area orange or reddish-orange, sometimes slightly brownish-orange posteriorly. Face, parafacials and parafrontals densely golden-yellow pollinose, the parafacials yellow in ground colour but the parafrontals blackish under the golden pollinosity. Ocellar setae well developed, usually very fine and slightly longer than upper reclinate frontal setae. Parafrontals without supernumerary

setae between upper and lower inclinate frontal setae (one specimen seen in which one such supernumerary seta is present on one side only). Antennae bright orange, third segment very long and about 4.5 to 4.8 times as long as second segment and falling short of mouth-margin by about one third or a quarter of its length; arista long-plumose on basal two fifths. Palpi pale yellow or whitish-yellow. Mentum dark brown or dark red-brown. *Thorax*: ground colour black, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and dorsum dark grey or dark bluish-grey pollinose, mesonotum sometimes brownish pollinose between the *dc* lines and with faint traces of three vittae. Presutural acrostichal hairs in two rows; without a distinct *dc* setula preceding the *prst dc* seta; two *post ia* setae present. *Wings*: entirely clear hyaline or with a small very faint brownish tinge preapically on anterior edge. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: yellow or reddish-yellow, fore coxae yellow or reddish-yellow under white pollinosity except at the extreme base and mid and hind coxae blackish with grey pollinosity. Fore tibia with two or three small *ad* setae (sometimes inconspicuous), the *pv* seta fine and somewhat shorter than distance from its insertion to apex of tibia. Mid coxa with very strong paired ventro-apical setae lying closely appressed; mid femur with one or two preapical *p* setae (!) [the holotype with one on one side and two on the other], the *pv* setae short and close-set towards the apex; mid tibia without an *ad* seta, the two *pd* setae about one or one and a half and two or two and a half times as long as tibial diameter. Hind femur with one very long submedian *pv* seta, the lower half medially of the *p* surface with numerous long fine hairs in some specimens but in others only with a few very short minute spinous setae (as in holotype); hind tibia without a preapical lobe, *without the normal proximal pd seta*, with a long strong *pv* seta which is slightly hooked at the apex and inserted at about one third from the base and followed by a row of about six smaller *pv* setae which decrease in size distally (Fig. 17), also with some stout *v* setulae in the apical quarter, the *d* preapical seta about three-quarters as long as hind metatarsus; hind tarsus simple. *Abdomen*: slightly laterally compressed towards the apex, T5 produced into a prominent dorsal keel, lateral lobes of sternite 5 small and subtriangular. T1 + 2 and T3 yellow, in some specimens with a median brownish dorsal mark on both tergites or only on T3; T4 yellow laterally but mainly blackish-brown dorsally with narrow yellowish fore and hind margins and *very* thin traces of greyish pollinosity indicating the boundary between the median and sublateral spots; T5 blackish-brown in ground colour with very narrow pale yellowish hind margins, grey pollinose except on the semi-shining dorsal keel which is blackish-brown, without sublateral spots; T7 + 8 and epandrium blackish-brown with grey pollinosity, without spots. Venter yellow, lobes of sternite 5 and paralobes of hypopygium yellowish-brown or red-brown. T5 laterally with numerous dense short erect setae (Fig. 50) with some flattened lanceolate downswept setae dorso-laterally against the hind margin, the latter setae longer than the more ventral setae, area in front of the downswept dorso-lateral setae bare or with a few simple hairs, ventro-apical margins with numerous long fine sinuous bristles. Hypopygium (Fig. 87) with long paralobes which are broadened in the apical two-thirds and bear some very long fine hairs on the posterior margins, mesolobe with only a few long hairs in some specimens

but in others with dense hairs. *Measurements*: body length 5.4 mm (range 5.2 to 5.5 mm), wing length 5.3 mm (range 5.2 to 5.5 mm) [4 specimens].

[♀. Not certainly known because of the difficulty of correct association with the ♂. Numerous females have been seen from New Guinea (material in Bishop Mus. and B.M.Nat.Hist. and listed below) which are probably those of *absentiseta* and which closely resemble the ♀ of *P. respondens* (Walker); these females have black-brown femora and fore coxae which are reddish-yellow in ground colour, the sublateral "spots" of the intermediate abdominal tergites extending round to the ventral surface of the abdomen (not with slightly darkened fore coxae and ventrolateral abdominal spots separated from the sublateral spots as in typical specimens of *respondens*).]

Affinities

P. absentiseta is very closely allied to *P. maculigera* (Stein) as shown by the general resemblance in the ♂ hypopygium and tergite 5 but is easily distinguished (♂) from this and all other known species by the absence of the proximal *pd* seta of the hind tibia. In some specimens the hind femur on the middle part of the posterior surface is bristled with long fine bristly hairs and in others with only a very few minute spine-like setae; the significance of this is not clear and it is possible that two sympatric sibling species are involved. In specimens with bristly hairs on the hind femur the mesolobe of the hypopygium is also densely haired, whereas in specimens with a few spines on the ventral part of the *p* surface of the hind femur there are only one or two hairs on the mesolobe. However, all specimens agree in lacking the proximal *pd* seta of the hind tibia and in the characteristic bristling of T 5 and for the present it is best to regard all as conspecific (the holotype has the sparsely haired mesolobe and hind femur with a few minute spines on the ventral half of the *p* surface of the hind femur).

Material examined

Holotype ♂, DUTCH NEW GUINEA: Vogelkop, Sacramba Vill., W. of Lake Anggi Giji, 1850 m., 1.viii.1957 (*D. E. Hardy*). In the Bernice P. Bishop Museum, Honolulu. Paratypes: 1 ♂, DUTCH NEW GUINEA: Wisselmeren, Enarotadi, 1900 m., 1.viii.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♂, N.E. NEW GUINEA: Papua, S. Highlands, N. of Mendi, 1800 m., 8.viii.1958 (*J. L. Gressitt*) (B.M.Nat.Hist.); 1 ♂, N.E. NEW GUINEA: Sepik-Waghi Div., N. of Banz, 1900 m., 11.vii.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.); 1 ♂, N.E. NEW GUINEA: Daulo Pass, Asaro-Chimbu Div., 3000 m., 13.vi.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.); 1 ♂, N.E. NEW GUINEA: Goroka-Kabebe, 1800 m., 20.vi.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♂, N.E. NEW GUINEA: Swart Val., Karubaka, 1450 m., 17.xi.1958 (*J. L. Gressitt*) (Bishop Mus.).

In addition the following female material has been examined which may belong to *P. absentiseta*; at present it cannot be established that these females are correctly associated with the male type material. N.E. NEW GUINEA: 4♀♀, Minj area, 1700 m., 3.vii.1957 (*D. E. Hardy*) (Bishop Mus. and B.M.Nat.Hist.); 3♀♀, S. Highlands, Mendi, 1660 m., 6.x.1958 (*J. L. Gressitt*) (Bishop Mus.); 1 ♀, S. Highlands, Aiyuro nr. Mendi, 1530 m., 7.x.1958 (*J. L. Gressitt*) (Bishop Mus.); 1 ♀, Goroka, 1530 m., 30.iv. to 3.v.1959 (*C. D. Michener*) (Bishop Mus.); 2♀♀, Maprik, 150 m., 1.i.1960

and 29.xii.1959 to 17.i.1960 (*T. C. Maa*) (Bishop Mus.); 4 ♀♀, Kassam, 48 km. E. of Kainantu, 1350 m., 28.x. and 7.xi.1959 (*T. C. Maa*) (Bishop Mus. and B.M. Nat.Hist.); 2 ♀♀, Okapa, 64 km. S. of Kainantu, 1800 m., 29.ix.1959 (*T. C. Maa*) (B.M.Nat.Hist.); 1 ♀, Tapibagar, upper Jimmi V., 1400 m., 19.vii.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♀, W. Highlands, Goiburung, E. of Korn Farm, 1560–1650 m., 16.x.1958 (*J. L. Gressitt*) (Bishop Mus.).

Distribution

Widespread in New Guinea, but not known from elsewhere.

Pygophora howeana Paramonov, 1961

Pygophora howeana Paramonov, 1961, *Ann. Mag. nat. Hist.* (13) 3: 510. Holotype ♂, LORD HOWE ISLAND. In the Division of Entomology Museum, C.S.I.R.O., Canberra.

Diagnosis

♂. Hind tibia without preapical lobe but T5 forming a prominent dorsal keel (though not very strongly flattened), parafrontals with a strong pair of supernumerary inclinate setae between the upper and lower pairs of inclinate frontal setae, hind tibia with a row of four or five *pv* setae along most of its length, hypopygium as in Fig. 88.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area deep orange-yellow. Face, parafacials and parafrontals golden-yellow pollinose. Ocellar setae well developed, longer and finer than upper reclinate frontal setae. Parafrontals with a pair of strong supernumerary inclinate setae between upper and lower pairs of inclinate frontal setae. Antennae orange, third segment about 3.0 times as long as second segment and falling short of mouth-margin by a little over half its length; arista long-plumose on basal two-fifths. Palpi creamy-white. Mentum dark red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely pale grey pollinose, dorsum densely greyish-yellow pollinose, mesonotum without vittae. Presutural acrostichal hairs in two rows, the hairs very strong and setulose; *prst dc* seta preceded by a small distinct *dc* setula about equal in size to *prst acr* setulae; two strong *post ia* setae present. *Wings*: with a very faint greyish smokiness anteriorly towards the apices but without definite brown spot. Calyptrae pale yellowish-white with white fringes. Halteres yellow. *Legs*: entirely yellow except for the mid and hind coxae which are reddish-black with pale grey pollinosity. Fore tibia with two small *ad* setae, the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia. Mid coxa with the paired ventro-apical setae equally developed, strong and close together. Mid femur with two preapical *p* setae, with three long *pv* setae in basal three-quarters and several small close-set *pv* setulae near the apex; mid tibia without an *ad* seta, the two *pd* setae two and three times as long as tibial diameter. Hind femur with two long strong *pv* setae in basal half; hind tibia without a preapical lobe, with four or five well developed *pv* setae inserted along most of its length except near the base, the *d* preapical

seta only very slightly shorter than hind metatarsus; hind tarsus simple. *Abdomen*: slightly laterally compressed towards the apex, T5 forming a more or less prominent dorsal keel but the keel not very strongly flattened, slightly subconical, in side view much higher than T7 + 8, lateral lobes of sternite 5 small and subtriangular with the projecting ventral part densely covered with small bristly hairs. T1 + 2 and T3 yellow, T3 with a dark red-brown median longitudinal mark; T4 yellow laterally but largely dark in ground colour dorsally with well developed black-brown median and sublateral spots which are separated by densely grey pollinose areas, the median spot triangular; T5 all dark in ground colour and densely greyish-yellow pollinose with a pair of small black sublateral spots and the dorsal keel indistinctly blackish-brown; T7 + 8 blackish-brown in ground colour with dense greyish-yellow pollinosity, without spots; epandrium dark apically with grey pollinosity, reddish ventrally. Venter pale yellow, lobes of sternite 5 and paralobes of hypopygium semi-translucent reddish-yellow. T5 with very long slightly flattened but very fine setae on the dorsal keel which are directed backwards, dorso-laterally and laterally with numerous very fine and long hair-like setae which stand out from the surface of the tergite and are curved upwards, ventro-apical marginal setae long and close-set, ventral edges of the tergite with dense bristly hairs; T7 + 8 with numerous very fine and long slightly sinuous hair-like setae generally similar to those on T5 but longer and less regularly upcurved. Hypopygium as in Fig. 88, paralobes very long but not greatly expanded apically. *Measurements*: body length 6.0 mm, wing length 5.8 mm [1 specimen].

♀. Generally similar to ♂ with the same yellow femora and strong third pair of inclinate frontal setae, but hind tibia without *pv* setae. Abdomen with T1 + 2 mainly yellowish but dorsally with an indefinite median dark brown area and some thin greyish pollinosity; T3 and T4 only very narrowly yellowish along hind margins, otherwise dark in ground colour with extensive greyish pollinosity and each with bold blackish-brown median and sublateral spots, the latter small but elongate and not nearly reaching to sides of the tergite, median spots more or less forming a dark median vitta; T5 with dark ground colour and yellowish-grey pollinosity, with a pair of well marked blackish-brown sublateral spots but without a median spot (although the centre of the tergite is extensively darker yellowish-brown pollinose); tergites without ventro-lateral spots. T4 without median discal setae, the marginal setae moderately strong and semi-recumbent (only middle ones more erect), T5 with a pair of short strong median discal setae (in specimen seen) standing on posterior half of median brownish pollinose area in addition to the pair of lateral discal setae standing on the sublateral spots. *Measurements*: body length 6.8 mm, wing length 6.4 mm [1 specimen].

Affinities

P. howeana is closely allied to *P. maculigera* (Stein) and *P. majalis* Paramonov. I have not seen the ♂ of *P. caledonica* (Bigot) and so have not been able to compare it with *howeana*, but Paramonov (1961) considers *howeana* to be closely related to *caledonica* as well as *maculigera*.

Material examined

Paratype ♂ and paratype ♀, LORD HOWE ISLAND: Lord Howe Island (N.S.W.),

24 and 30.xi.1955 (*S. J. Paramonov and Z. Liepa*) (Div.Ent.Mus.Canberra).

I have not seen the holotype specimen which has the same data as the paratypes examined except for the date, 28.xi.1955.

Distribution

Known only from the type series from Lord Howe Island and probably an endemic species confined to this island.

Pygophora luteicornis (Walker, 1859) **comb. n.**

Caenosia luteicornis Walker, 1859, *J. Proc. Linn. Soc.* 3: 108. Holotype ♂, ARU ISLANDS. In the British Museum (Natural History), London.

Diagnosis

Very large species, ♂ distinguished from all other known species by presence of *pv* setae on *mid* tibia and by the comb of strong curved spines on apical half of *pv* surface of hind femur.

Description

♂. *Head*: occiput pale grey or slightly yellowish-grey pollinose. Interfrontal area yellow-orange. Face, parafacials and parafrontals all densely golden-yellow pollinose, parafrontals therefore not noticeably contrasting in colour with interfrontal area. Ocellar setae well developed, about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright yellow-orange, very long, third segment 4.75 times as long as second segment and falling short of mouth-margin by about one-fifth of its length; arista long-plumose on basal half. Palpi yellowish-white. Mentum dark red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae, mesonotum and scutellum entirely grey pollinose, mesonotum without trace of vittae. Presutural acrostichal hairs in two rows; the *dc* setula preceding *prst dc* seta not distinctly differentiated; two distinct *post ia* setae present. *Wings*: with a large apical brown mark which reaches from well before apex of R_{2+3} to wing tip and extends backwards to about mid way between vein R_{4+5} and M_{1+2} and with a very faint trace of brownish suffusion on the apical part of vein M_{1+2} . Calyptrae white with white fringes. Halteres yellowish-white. *Legs*: entirely yellow except for mid and hind coxae which are reddish-black with thin grey pollinosity. Fore tibia with *pv* seta long, about three-quarters or seven-eighths as long as distance from its insertion to apex of tibia, with two or three small *ad* setae, and with long fine semi-erect hair on outer surface. Mid femur with two preapical *p* setae, without specialised bristling, two long *pv* setae in basal half; mid tibia without an *ad* seta, with an irregular row of six to eight *pv* setae (Fig. 21) of which one or two are in the basal half, the two *pd* setae one and two times as long as tibial diameter. Hind femur with one very long *pv* seta in basal half and with a *pv* row of long strong curved spines in the apical half; hind tibia without a preapical lobe and without *pv* setae, setae short, the *d* preapical seta about half as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 49): laterally compressed towards the apex, T5 produced

into a strongly flattened dorsal keel and T7 + 8 also produced into a slightly flattened acuminate apex, lateral lobes of sternite 5 large and acuminate ventrally. T1 + 2 reddish-yellow laterally and dorsally in posterior half, basal half dorsally dark brown, the dark colour extending backwards in the mid-line as a red-brown mark which more or less reaches hind margin, yellowish areas dorsally with thin white pollinosity; T3 reddish-yellow with thin white pollinosity along the basal and apical margins and with a large bold brown median spot; T4 reddish-yellow laterally with basal and apical thin white pollinosity, dorsally with a very large black-brown median spot and two very small indistinct sublateral spots, areas between median and sublateral spots and behind the sublateral spots white pollinose; T5 entirely dark in ground colour except for an extremely narrow yellowish apical margin and with pale greyish-white pollinosity, dorsal keel and a pair of diffuse sublateral spots blackish-brown; T7 + 8 dark reddish-brown in ground colour with pale grey pollinosity, slightly yellowish-brown on dorsal apex. First three sternites yellow, sternite 5 yellowish-brown. T5 with a pair of long backwardly-projecting setae on dorsal keel, dorso-laterally with a series of long flattened outwardly and downwardly-directed setae, laterally with very numerous flattened and slightly upcurved setae, ventro-apically with a dense tuft of setae; T7 + 8 with outstanding flattened setae as on T5, with one strong ventro-apical seta on either side and posteriorly with some backwardly-directed hairs. *Measurements*: body length 7.0 mm, wing length 6.2 mm [1 specimen].

♀. Unknown. Walker (1860, p. 141) described a ♀ which he doubtfully considered to be that of *luteicornis*. The specimen no longer exists and Walker's description suggests that it probably was not the ♀ of *P. luteicornis*.

Affinities

A distinctive and easily-recognised species not very closely allied to other species but the abdominal structure and bristling suggests some affinity with *P. apicalis* and related species such as *P. maculigera* (Stein); it differs from *P. apicalis* in lacking a preapical lobe on the ♂ hind tibia. The possession of *pv* setae on the mid tibia, or the strong *pv* spines of the hind femur, distinguish *P. luteicornis* from other species.

Material examined

Holotype ♂, INDONESIA: Aru Islands, — (A. R. Wallace). DUTCH NEW GUINEA: 1 ♂, Lake Sentani, Iffar., viii.1936 (*L. E. Cheesman*) (B.M.Nat.Hist.).

Distribution

Known only from the two localities mentioned above in the extreme east of Indonesia and on the north coast of New Guinea.

Pygophora compressiventris (Thomson, 1869) *comb. n.*

Coenosia compressiventris Thomson, 1869, *Eugenies Resa*: 559. Holotype ♂, "MALACCA". In the Naturhistoriska Riksmuseum, Stockholm.

Pygophora norrisi Paramonov, 1961, *Ann. Mag. nat. Hist.* (13) 3: 508. Holotype ♂, QUEENSLAND. In the Division of Entomology Museum, C.S.I.R.O., Canberra. *Syn. n.*

Diagnosis

Small species, ♂ with compressed abdomen and T5 produced into a prominent dorsal keel, sides of T5 and T7 + 8 with numerous outstanding slightly flattened setae, T4 without distinct median spot, lateral lobe of sternite 5 as in Fig. 109, paralobe of hypopygium as in Fig. 89, hind tibia without preapical lobe, antennae short, wing with preapical brown spot. ♀ with yellow femora as ♂ (cf. *P. hopkinsi* Malloch).

Description

♂. *Head*: occiput greyish-white pollinose. Interfrontal area pale lemon yellow. Face and parafacials yellowish-white pollinose, parafrontals very pale yellow pollinose. Ocellar setae short and very fine, about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellow (second segment slightly orange-yellow), third segment short, about 2.4 times as long as second segment and falling short of mouth-margin by about two-fifths of its length; arista long-plumose on basal half. Palpi white. Mentum dark yellow-brown. *Thorax*: ground colour entirely dark brown or blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, dorsum pale yellowish or yellowish-grey pollinose without vittae. Presutural acrostichal hairs in two rows; no distinct *dc* setula differentiated in front of *prst dc* seta; two *post ia* setae present, the anterior one small and very fine. *Wings*: mainly hyaline but with a distinct dark brown suffusion on the apex of vein R_{2+3} which extends less distinctly on to the preapical part of vein R_{4+5} . Calyptrae whitish with white fringes. Halteres pale yellow. *Legs*: entirely yellow including the coxae. Fore tibia with two very small *ad* setae, the *pv* seta fine and nearly as long as distance from its insertion to apex of tibia. Mid coxa with the paired ventro-apical setae very strong and closely applied to one another so that together they form a strong "spur"; mid femur with two preapical *p* setae, without specialised bristling, median third with three long fine *pv* setae of which the middle one is longest; mid tibia without an *ad* seta, the two *pd* setae one and a half and two times as long as tibial diameter. Hind femur with one or two long *pv* setae; hind tibia without a preapical lobe, with a row of four or five small *pv* setae (of which the basal one or two are the strongest and occur on the basal half of the tibia), the *d* preapical seta about three-fifths as long as the hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 52): strongly laterally compressed towards the apex with the dorsum of T5 produced into a prominent flattened keel, lateral lobes of sternite 5 of medium size and shaped as in Fig. 109. T1 + 2, T3 and T4 yellow, T4 with a trace of yellowish-brown sublateral spots and sometimes a yellowish-brown median spot also; T5 yellowish with the dorsal keel blackish-brown or dark yellowish-brown but without sublateral spots or with only very faint traces of such spots; T7 + 8 reddish-yellow with a faint median dorso-apical brownish mark; epandrium reddish-yellow with very thin whitish pollinosity. Venter, lateral lobes of sternite 5, and paralobes of hypopygium yellow. T5 with very long backwardly and slightly downwardly directed flattened setae on the dorsal keel and dorso-laterally with numerous long slightly flattened and upcurved setae which stand out erect from the surface of the tergite, ventro-apical marginal setae of T5 very weak; T7 + 8 with numerous

erect flattened setae similar to those on T5. Hypopygium as in Fig. 89. *Measurements*: body length 3.9 mm, wing length 4.1 mm [1 specimen].

♀. Femora yellow as in ♂, but wings without the preapical brown spot and hind tibiae without *pv* setae. Abdomen normal, T1 + 2 and T3 yellow, T3 with a pair of pale yellow-brown sublateral spots but without a median spot; T4 partly yellow and with very large dark yellowish-brown or reddish-brown median and sublateral spots which are separated by yellowish-grey pollinose areas, ventro-laterally with a very indistinct reddish-brown area; T5 more or less reddish-brown in ground colour anteriorly with yellowish-grey pollinosity, reddish-yellow apically, with a pair of distinct reddish-brown sublateral spots and with a less distinct reddish-brown median line. T4 and T5 without median discal setae. *Measurements*: body length 4.4 mm, wing length 4.0 mm [1 specimen].

Affinities

Very closely allied to *P. hopkinsi* Malloch, with very similar abdominal form and bristling and very similar hypopygium and sternite 5 in the ♂. The ♀ is very easily distinguished from *hopkinsi* by the all-yellow femora (almost entirely blackish-brown in *hopkinsi*), and the ♂ is distinguished by the much shorter antennae and whitish face, and by differences in the shape of the paralobes and the lateral lobes of sternite 5.

Material examined

Coenosia compressiventris Thomson, holotype ♂, "MALACCA" (presumably Malaya, but no other data). *Pygophora norrisi* Paramonov, paratype ♂ and paratype ♀, AUSTRALIA: Queensland, Alligator Creek nr. Mackay, 7.v.1955 (*K. R. Norris*) (♂ in B.M.Nat.Hist., ♀ in Div.Ent.Mus.Canberra). AUSTRALIA: 1 ♂, 1 ♀, Queensland, Townsville, 1909 (*F. P. Dodd*) (B.M.Nat.Hist.). INDONESIA: 1 ♂, Lombok, Sembaloen, 30–31.iii.1927 (*Sunda Expedition*) (D.Ent.Inst.).

In addition I have seen the following female specimens which may belong to this species: 1 ♀, PHILIPPINE ISLANDS: Leite, Kalambugan, 1.ii.1915 (—) (U.S. Nat.Mus.); 1 ♀, DUTCH NEW GUINEA: Vogelkop, Manokwari, 75 m., 22.vii.1957 (*D. E. Hardy*) (Bishop Mus.); and 1 ♀, N.E. NEW GUINEA: Maprik, 150 m., 29.xii.1957 to 17.i. 1960 (*T. C. Maa*) (Bishop Mus.).

Distribution

From "Malacca" to Queensland, but records are few. The ♂ genitalia of a Queensland specimen have been very carefully compared with the ♂ genitalia (slide mounted) of Thomson's type of *compressiventris* and the genitalia (and every other character) are identical. Paramonov (1961) recently described the species as *P. norrisi*, but this name must be synonymised with *compressiventris* Thomson.

Pygophora hopkinsi Malloch, 1929

Pygophora hopkinsi Malloch, 1929, *Insects of Samoa* pt. 6, 3: 161. Holotype ♂, SAMOA. In the British Museum (Natural History), London.

Diagnosis

Small species, ♂ with laterally compressed abdomen and T5 produced dorsally

into a prominent keel, sides of T5 and T7 + 8 with long outstanding narrow flattened lanceolate setae, lateral lobe of sternite 5 as in Fig. 108, paralobe of hypopygium as in Fig. 90, hind tibia without a preapical lobe, antennae long and pollinosity of face yellow. ♀ with femora blackish-brown or dark brown on basal two-thirds or four-fifths, only the apices yellow (cf. *P. compressiventris* (Thomson)).

Description

♂. *Head*: occiput pale greyish-white pollinose. Interfrontal area deep yellow or orange-yellow. Face, parafacials and parafrontals bright yellow or pale yellow pollinose, ocellar triangle and vertex more greyish-yellow pollinose. Ocellar setae very fine, about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright orange-yellow or bright yellow, third segment long, about 3.7 times as long as second segment and falling short of mouth-margin by about one-sixth of its length; arista long-plumose on basal half. Palpi yellowish-white. Mentum reddish-brown or dark yellowish-brown. *Thorax*: ground colour entirely blackish or reddish-white, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, dorsum pale grey or yellowish-grey pollinose and in some lights with a slight trace of blackish vittae. Presutural acrostichal hairs in two rows; no *dc* setula distinctly differentiated in front of the *prst* seta; two *postia* setae present. *Wings*: entirely hyaline or with a dark brown suffusion on the apex of vein R_{2+3} and R_{4+5} . Calyptrae white with white fringes. Halteres yellow. *Legs*: entirely yellow, only the mid and hind coxae sometimes slightly reddish or blackish. Fore tibia with two small *ad* setae, the *pv* seta long and fine and almost equal in length to distance from its insertion to apex of tibia. Mid coxa with the paired ventro-apical setae very strong and closely appressed to each other so that they form a strong "spur"; mid femur with two preapical *p* setae, without specialised bristling, with only one or two fine *pv* setae in median third; mid tibia without an *ad* seta, the two *pd* setae about one and two times as long as tibial diameter. Hind femur with two very fine submedian *pv* setae; hind tibia without a preapical lobe, with four or five small *pv* setae along its length, the *d* preapical seta about two-thirds as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 51): strongly laterally compressed towards the apex with the dorsum of T5 produced into a prominent flattened keel, lateral lobes of sternite 5 of medium size and shaped as in Fig. 108. T1 + 2 and T3 yellow with paler pollinose hind margins, T3 sometimes with indefinite traces of a pale reddish-brown median mark; T4 only yellowish or reddish-yellow ventro-laterally, dorsally largely darkish in ground colour with a large broad dark reddish-brown, dark brown or blackish-brown median spot and a pair of large dark red-brown or nearly black sublateral spots, the sublateral spots separated from the median spot by well marked longitudinal grey pollinose areas and the areas immediately outside the sublateral spots also indefinitely greyish pollinose, dorsal hind margin of the tergite pale yellowish; T5 partly dark in ground colour dorsally with dense grey pollinosity, but yellowish ventro-laterally, the dorsal keel dark brown or blackish-brown but sublateral spots absent or only very faintly indicated in certain lights; T7 + 8 mainly reddish-yellow with thin whitish pollinosity, sometimes darker reddish-brown in ground colour dorsally, without spots but sometimes distinctly brownish dorso-apically;

epandrium yellowish-orange with thin white pollinosity. Venter and lateral lobes of sternite 5 reddish-yellow, paralobes of hypopygium orange-yellow. T5 with very long backwardly-directed flattened setae on the dorsal keel, dorso-laterally with a row of long flattened setae standing out erect from the surface and laterally with shorter very numerous flattened lanceolate setae which stand out erect from the surface and are curved upwards, ventro-apical marginal setae of T5 very long but fine; T7 + 8 dorsally and laterally with numerous long upcurved lanceolate setae similar to those on T5. Hypopygium as in Fig. 90. *Measurements*: body length 3.6 mm (range 3.4 to 3.8 mm), wing length 3.25 mm (range 3.1 to 3.3 mm) [6 specimens].

♀. Differs very noticeably from ♂ by having all femora dark brown or blackish-brown on basal two-thirds or four-fifths (only the apices yellow); antennae shorter than in ♂, fore coxae reddish-brown, wings always without brown spot, hind tibiae without *pv* setae, three brownish mesonotal vittae sometimes distinct. Abdomen normal, T1 + 2 yellow; T3 sometimes extensively yellowish laterally but usually only narrowly yellowish on hind margin and ventrally against the anterior margin, dorsally with very large bold reddish-brown or black-brown median and sublateral spots which are separated and more or less surrounded by yellowish or yellowish-grey pollinosity, the median spot usually parallel-sided and elongate, the sublateral spots more or less continuing laterally as a brownish band around to the ventral surface; T4 similar to T3 with very large bold blackish-brown median and sublateral spots, the median spot elongate and parallel-sided, the sublateral spots continuing round the sides of the tergite as a brownish band, areas between median and sublateral spots densely grey or yellowish-grey pollinose, hind margin of tergite narrowly yellowish; T5 mainly dark in ground colour with grey pollinosity and a pair of blackish-brown sublateral spots, somewhat yellowish-brown pollinose in the mid-line. T4 and T5 without median discal setae. *Measurements*: body length 3.9 mm (range 3.6 to 4.2 mm), wing length 3.5 mm (range 3.2 to 3.7 mm) [11 specimens].

Affinities

P. hopkinsi is closely allied to *P. compressiventris* (Thomson) and *P. lepidofera* (Stein). The ♂ is easily distinguished from *lepidofera* by the lanceolate (instead of spatulate scale-like) setae of T5, and from *compressiventris* by differences in the shape of the lateral lobes of sternite 5 and the paralobes. The ♀ differs from *compressiventris* in having blackish-brown femora and very well developed large dark spots on T3, but the females of *hopkinsi* and *lepidofera* are almost indistinguishable as both species have dark femora and the same abdominal pattern; in the material seen, however, of *lepidofera* ♀ the parafrontals are black in ground colour with greyish-white pollinosity (strongly contrasting in appearance with the yellowish-orange interfrontal area), whereas in *hopkinsi* ♀ the parafrontals are yellowish in ground colour like the parafacials with yellow pollinosity (not strongly contrasting in appearance with the interfrontal area). *P. hopkinsi* varies slightly over its extensive range (I can find no important distinction between material from Ceylon and the type series from Samoa) and males from Ceylon lack the dark brown wing-spot which occurs in specimens from the western Pacific (males seen from Sumatra, Philippines and northern Queensland also lack the dark spot).

Material examined

Holotype ♂, SAMOA: Tutuila, Pago Pago, 14.xii.1925 (*P. A. Buxton and G. H. Hopkins*). Paratype ♀, data as for holotype (B.M.Nat.Hist.); paratype ♀, SAMOA: Upolu, Malololelei, 2000 ft., xii.1925 (*P. A. Buxton and G. H. Hopkins*) (B.M.Nat.Hist.); paratypes 2 ♀♀, SAMOA: Savaii, Safune, 13.v.1924 (*E. H. Bryan*) (B.M.Nat.Hist.). CEYLON: 6 ♂♂, 6 ♀♀, Kandy, Roseneath, 8.ii.1954 (*F. Keiser*) (Nat.Mus.Basel and B.M.Nat.Hist.); 1 ♀, Kandy, Roseneath, 13.viii.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Kandy, 5.x.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Kandy, 18.ii.1954 (*F. Keiser*) (B.M.Nat.Hist.); 1 ♀, Kandy, L. Blake's Drive, 16.xii.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, Nikaweratiya, 23.i.1954 (*F. Keiser*) (Nat.Mus.Basel). SUMATRA: 1 ♂, Fort de Kock, 920 m., 1925 (*E. Jacobson*) (U.S.Nat.Mus.); 3 ♀♀, Brastagi, v.1927 (*F. J. Meggitt*) (U.S.Nat.Mus.). AUSTRALIA: 1 ♂, Queensland, Innisfail, — (*J. F. Illingworth*) (U.S.Nat.Mus.). BISMARCK ARCHIPELAGO: 1 ♂, Admiralty Islands, Manus, 17.iv.1932 (*J. L. Froggatt*) (B.M.Nat.Hist.). PHILIPPINE ISLANDS: 2 ♀♀, Leite, Kalambugan, 1.ii.1915 (—) (U.S.Nat.Mus.); 1 ♀, Los Banos, — (*P. I. Baker*) (U.S.Nat.Mus.); 1 ♀, Luzon, Mt. Makiling, — (*Baker*) (U.S.Nat.Mus.). SOLOMON ISLANDS: 1 ♂, 1 ♀, Guadalcanal, Lunga, 1936 (*R. A. Lever*) (B.M.Nat.Hist.). NEW HEBRIDES: 1 ♂, Malekula, Atchin Is., vii.1929 (*L. E. Cheesman*) (B.M.Nat.Hist.). SAMOA: 1 ♂, 2 ♀♀, Tutuila, Leone Rd., 19.ii.1927 (*E. H. Bryan*) (Bishop Mus.); 1 ♀, Tutuila, Pago Pago, 18.iv.1924 (*E. H. Bryan*) (Bishop Mus.); 3 ♂♂, Savaii, Safune, 12–13.v.1924 (*E. H. Bryan*) (Bishop Mus.); 1 ♂, Upolu, Malololelei, 8.vii.1925 (*G. P. Wilder*) (Bishop Mus.); 1 ♀, Upolu, Malololelei, 19.vii.1925 (*G. P. Wilder*) (Bishop Mus.); 1 ♀, Tau, Manua, 20.ii.1926 (*A. F. Judd*) (Bishop Mus.).

Distribution

A widespread species occurring from Ceylon eastwards to Samoa (the type locality), but unknown from Fiji—there being an apparent break in distribution between New Hebrides and Samoa. It appears not to occur on Formosa where its place seems to be taken by *P. lepidofera* (Stein), and I have seen no material from the mainland of south-east Asia. Only one specimen has been seen from northern Queensland and it is doubtful whether the species is fully established in Australia. Paramonov (1961) does not record it from there.

Pygophora lepidofera (Stein, 1915) **comb. n.**

Coenosia lepidofera Stein, 1915, *Suppl. ent. Berl.* 4: 50. Lectotype ♂, FORMOSA. In the Deutsches Entomologisches Institut, Berlin.

Lectotype designation: Stein described *C. lepidofera* from one ♂ and three ♀ syntypes (all in D.Ent.Inst.). The ♂ syntype has been selected and labelled as lectotype and the ♀ syntypes have been labelled as paralectotypes.

Diagnosis

Very small species; ♂ with T5 laterally compressed and forming a dorsal keel and bearing laterally a number of remarkable large leaf-like scales (Fig. 53), hind tibia in the middle third with a row of four long fine subequal *pv* setae (Fig. 18),

mid femur with one conspicuous and isolated strong *pv* seta at about two-fifths from the apex. ♀ with femora almost entirely dark brown and parafrontals black in ground colour.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area reddish-yellow, darkening slightly posteriorly. Face whitish pollinose over a reddish-brown ground colour, parafacials yellowish-white pollinose over a yellow ground colour, parafrontals blackish in ground colour (therefore strongly contrasting in colour with the interfrontal area) with whitish pollinosity, the pollinosity appearing rather greyish because of the underlying dark colour. Ocellar setae about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellowish-orange, third segment about 2.5 times as long as second segment and falling short of mouth-margin by about a third of its length; arista long-plumose on basal two-fifths. Palpi yellowish-white. Mentum reddish-brown. *Thorax*: ground colour entirely reddish-black, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, dorsum pale yellowish-grey pollinose without vittae. Presutural acrostichal hairs in two rows; *prst dc* seta not preceded by a distinctly differentiated *dc* setula; two *post ia* setae present. *Wings*: entirely hyaline. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow, except for the mid and hind coxae which are reddish or reddish-black with pale grey pollinosity. Fore tibia with two very small inconspicuous *ad* setulae, the *pv* seta very fine and about two-thirds as long as distance from its insertion to apex of tibia. Mid coxa with the paired ventro-apical setae closely appressed to one another, stout basally but strongly tapering and very fine apically; mid femur with two preapical *p* setae, without specialised bristling, with an isolated conspicuous long and rather strong *pv* seta at about two-fifths from the apex; mid tibia without an *ad* seta, the two *pd* setae one and two times as long as tibial diameter and the proximal one very small. Hind femur with two submedian *pv* setae of which the basal one is short and strong and the apical one longer and finer; hind tibia without a preapical lobe, with four long fine subequal *pv* setae in the median third (Fig. 18) and with several short *pv* setulae nearer the apex, the *d* preapical seta only a little over half as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 53): with T5 strongly laterally compressed and forming a slightly flattened dorsal keel, lateral lobes of sternite 5 small. T1 + 2 and T3 yellowish with paler yellowish-white hind margins; T4 partly yellowish but dorsally with a subtriangular yellow-brown median spot and indistinct pale yellow-brown sublateral spots which merge into the yellowish ground colour, areas between the spots white pollinose; T5 dark brown in ground colour dorsally with greyish-white pollinosity, without sublateral spots but the median keel slightly shining dark yellowish-brown, the tergite reddish-yellow ventrolaterally; T7 + 8 and epandrium reddish-brown in ground colour with pale grey pollinosity. Venter, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. T4 with the hairs on the sides unusually numerous; T5 laterally with a number of large dark brown leaf-like scales (modified setae) which stand out erect from the surface, ventrally with numerous long bristly hairs but the ventro-apical marginal setae not regularly arranged as in most species; T7 + 8 with numerous

very fine hairs antero-laterally but without scales. Hypopygium with paralobes narrow basally but broadened towards the apices. *Measurements*: body length 3.5 mm, wing length 3.2 mm [1 specimen].

♀. Differs from the ♂ by having all femora dark brown on basal three-quarters (yellow only at the apices) and by lacking *pv* setae on hind tibia; parafrontals as in ♂ but the black ground colour more distinct, the parafrontals contrasting in colour with the orange-yellow interfrontal area. Abdomen normal, T1 + 2 yellow with an indefinite darkened area medially; T3 partly reddish-yellow (mainly ventrally and on the hind margin) with large dark reddish-brown or blackish-brown median and sublateral spots separated by grey pollinose areas, the ground colour dark under the grey pollinose areas and the median spot elongate and parallel-sided; T4 similar to T3 with very large bold blackish-brown median and sublateral spots, the median spot more or less parallel-sided and extending the length of the tergite, hind margin narrowly pale yellowish; T5 dark in ground colour with grey pollinosity and a pair of black-brown sublateral spots, the median line narrowly yellowish-brown pollinose. T4 and T5 without median discal setae. *Measurements*: body length 3.7, 3.8 mm, wing length, 3.4, 3.5 mm [2 specimens].

Affinities

P. lepidofera is allied to *P. hopkinsi* Malloch and *P. compressiventris* (Thomson) but the ♂ is easily distinguished from these species, and from all other known species, by the curious leaf-like scales on the abdomen. The ♀ has dark femora (in contrast to *compressiventris* ♀) and is not easy to distinguish from the ♀ of *hopkinsi* although it appears to be consistently separable by the characters given in the key.

Material examined

Lectotype ♂, FORMOSA: north Paiwan District, Paroe, viii.1912 (*H. Sauter*). Paralectotypes: 3 ♀♀, same locality and collector as lectotype but date 7.ix.1912. RYUKYU ISLANDS: 1 ♂, Ishigaki I., 15–20.xii.1952 (*G. E. Bohart*) (B.M.Nat.Hist.); 1 ♀ with same data (Bishop Mus.).

Distribution

Only known from the above-listed material from Formosa and Ryukyu Islands.

Pygophora minuta Malloch, 1921

Pygophora minuta Malloch, 1921, *Ann. Mag. nat. Hist.* (9) 8: 239. Holotype ♂, QUEENSLAND. In the British Museum (Natural History), London.

Diagnosis

Extremely small species (length 3.4 to 3.7 mm); ♂ with outstanding long narrow lanceolate flattened scale-like setae on the sides of T4 as well as on T5 and T7 + 8 (Fig. 54), hypopygium as in Fig. 91, face dark brown and third antennal segments mainly brown.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area very pale yellow. Face

dark brown, only showing very thin whitish pollinosity in certain lights; parafacials and parafrontals densely whitish pollinose. Ocellar setae about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae with basal segments light orange-yellow, third segments yellow at the base but brown on apical three-quarters (possibly not a constant character), third segment about 2.75 times as long as second segment and falling short of mouth-margin by about one-sixth of its length; arista long-plumose on basal two-fifths. Mentum dark brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and dorsum densely grey pollinose, mesonotum without trace of vittae. Presutural acrostichal hairs in two rows; no *dc* setula differentiated in front of *prst dc* seta; two *post ia* setae present. *Wings*: entirely hyaline. Calyptrae white with white fringes. Halteres pale creamy-yellow. *Legs*: entirely yellow, only mid and hind coxae slightly reddish. Fore tibia with two very small *ad* setae, the *pv* seta about three-quarters as long as distance from its insertion to apex of tibia. Mid coxa with the paired ventro-apical setae stout and straight, lying very closely beside one another; mid femur with two preapical *p* setae, the *pv* surface with a very long strong submedian seta and with rather short stout *pv* setae between this long seta and the base; mid tibia without an *ad* seta, the two *pd* setae about one and one and a half times as long as tibial diameter. [Hind legs missing from ♂ type but hind tibia with normal bristling and without a preapical lobe (Malloch, original description)]. *Abdomen* (Fig. 54): distinctly laterally compressed towards the apex so that in dorsal view T5 is slightly narrower than T7 + 8, but T5 not produced dorsally into a prominent keel, lateral lobes of sternite 5 small and shaped as in Fig. 54. T1 + 2 more or less entirely and other tergites ventrolaterally pale reddish-yellow, hind margins of T3 and T4 also yellowish; most of T3 — T7 + 8 blackish in ground colour with grey pollinosity, T3 with traces of a dark brown median area and reddish-brown sublateral spots, T4 with a large black-brown median spot and a pair of large black sublateral spots, T5 with a very large dorsal median blackish-brown area but without sublateral spots, T7 + 8 without spots but dorso-apically somewhat brownish in certain lights; epandrium bright reddish-orange with a little thin whitish pollinosity (the colour of the epandrium contrasting with the dark T7 + 8). Venter reddish-black, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. T4, T5 and T7 + 8 laterally each with flattened narrow lanceolate scale-like setae those on T4 smaller than the others and directed slightly backwards, those on T5 and T7 + 8 longer and more conspicuous and standing out at right-angles to the surface; the ventro-apical marginal setae of T5 very few in number and mostly weak, only one of them on either side long and strong. Hypopygium as in Fig. 91. *Measurements*: body length 3.4 mm, wing length (approximately, as wings of type damaged) 3.2 mm [1 specimen].

♀. Face, parafacials and parafrontals densely grey pollinose, interfrontal area darker than in ♂ and antennae less brown apically. Abdomen with T1 + 2 mainly dirty yellowish but partly yellowish-brown dorsally and pale whitish-yellow laterally against the hind margin; T3 mainly dark in ground colour but hind margin narrowly pale yellowish, with a very large median and large rounded

sublateral black-brown spots, areas between and around the spots grey pollinose; T4 similar to T3 with dark ground colour except for pale hind margin, grey pollinosity and large blackish-brown median and sublateral spots; T5 dark with greyish pollinosity and a pair of large dark brown sublateral spots, pollinosity somewhat reddish medially. T4 without median discal setae but the marginal setae very large and strong, T5 without median discal setae but the lateral discal setae standing on the sublateral spots very strong. Measurements: body length 3.7 mm. wing length 3.4 mm [1 specimen].

Affinities

The flattened scale-like setae of the ♂ abdomen and small size indicate possible affinities with *P. hopkinsi* Malloch and *P. lepidofera* (Stein), but *minuta* differs from both these species in lacking a definite dorsal keel to T5, in the very different hypopygium, and in possessing flattened setae on T4 as well as the succeeding tergites. The ♀ is generally similar to that of *hopkinsi* but the femora are yellow and not blackish-brown; from *compressiventris* (Thomson) the ♀ may be distinguished by the large dark spots of T3 with surrounding grey pollinosity.

Material examined

Holotype ♂, AUSTRALIA: Queensland, Kuranda, 1100 ft., 21.vi. to 24.vii.1913 (*R. E. Turner*). AUSTRALIA: 1 ♀, Queensland, — (—) (B.M.Nat.Hist.).

Distribution

Known only from Queensland, Australia.

***Pygophora intermedia* sp. n.**

Note: Malloch recognised this species as new and labelled the only known male (U.S.Nat.Mus.) as "Pygophora intermedia Type det J. R. Malloch". This name was not published by Malloch, and I am here describing the new species using the appropriate name Malloch had chosen for it.

Diagnosis

♂. Hind tibia with a preapical lobe and *pv* setae but T5 of abdomen not produced into a very prominent laterally flattened dorsal keel (although it is slightly higher than T7 + 8), T5 and T7 + 8 dorsally with very long outstanding slightly flattened setae (Fig. 41).

Description

♂. *Head:* occiput pale grey pollinose, occipital setulae abundant and in five or six irregular rows. Interfrontal area bright yellow-orange. Face, parafacials and parafrontals yellow pollinose, parafrontals not noticeably contrasting with interfrontal area. Ocellar setae well developed, longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright yellow-orange, third segment very long and about 5.5 times as long as second segment, falling short of mouth-margin by about one-thirteenth of its length; arista long-plumose on basal two-fifths. Palpi pale yellow. Mentum dark orange-brown. *Thorax:* ground colour black, humeral

calli and scutellum concolorous with rest of mesonotum; pleurae and most of dorsum grey pollinose, mesonotum with three broad yellowish-brown pollinose vittae (one on either side outside the rows of *dc* setae and a median *acr* vitta). Presutural acrostichal hairs in two rows; a small *dc* setula present in front of the *prst dc* seta; two well developed *post ia* setae present. *Wings*: mainly clear hyaline but faintly brownish infusate on the apex of R_{2+3} . Calyptrae yellowish-white with white fringes. Halteres pale yellow. *Legs*: mainly yellow, fore coxae almost all yellowish but dark at extreme base, mid and hind coxae reddish-black with grey pollinosity. Fore tibia with two small *ad* setae, the *pv* seta long and about equal in length to distance from its insertion to apex of tibia. Mid coxa with paired ventro-apical setae well developed; mid femur with two preapical *p* setae, with a very strong *av* seta and a much smaller strong *av* seta near it in the middle third, *pv* surface with three very long strong setae in the middle third followed by a sparse comb of very short strong setae and some longer close-set *pv* setae near the apex; mid tibia without an *ad* seta, the two *pd* setae short and about one and one and a half times as long as tibial diameter. Hind femur with two very long *pv* setae in basal two-thirds; hind tibia with a large preapical lobe (Fig. 13) and with two *pv* setae near the middle, the *d* preapical seta incomplete in holotype but probably shorter than hind metatarsus; hind tarsus simple. *Abdomen*: very slightly laterally compressed towards the apex but T5 not forming a strongly flattened dorsal keel (although it is slightly prominent dorsally and stands higher than T7 + 8 when seen laterally), lateral lobes of sternite 5 large and subtriangular. Tergites rather shining; T1 + 2 and T3 reddish-yellow, each with a large median subquadrate dark reddish-brown area; T4 indefinitely reddish-orange ventro-laterally, dorsally with large bold blackish-brown median and sublateral marks separated by very obvious longitudinal grey pollinose areas, the median spot triangular and the sublateral spots extending round laterally to merge indefinitely with the reddish-orange lateral colour; T5 all dark in ground colour with blackish-brown median and sublateral spots, sides of tergite and areas between the spots yellowish-grey pollinose, the medio-lateral hollowings slightly blackish from some angles; T7 + 8 blackish with greyish or yellowish-grey pollinosity, only the dorso-apical angle slightly blackish; epandrium reddish-black with thin grey pollinosity. Venter indefinitely darkened with grey pollinosity, lobes of sternite 5 and paralobes of hypopygium shining reddish. T5 and T7 + 8 (Fig. 41) dorso-laterally with very long fine slightly flattened and upcurved outstanding setae, sides of these tergites with shorter erect flattened slightly lanceolate setae, ventro-apical margins of T5 with long dense bristles. Hypopygium with long paralobes, each having a very dense long fringe of black hairs on outer edge basally (hypopygium not removed from holotype and not figured). *Measurements*: body length 5.3 mm, wing length 5.8 mm [1 specimen].

♀. Resembling the ♂ but proximal halves of femora reddish-brown, wings without brownish suffusion on apices of R_{2+3} (although generally very faintly yellowish), hind tibia without preapical lobe or *pv* setae, antennae short. Abdomen with T1 + 2 and T3 mainly shining reddish-yellow, each with a median reddish-brown area, this area large and filling half the dorsal surface of the tergite on T3; T4 shining red-brown with two dorsal longitudinal very evident pale grey pollinose

lines which divide the reddish-brown colour into a median area and the lateral areas which extend over the whole sides of the tergite; T5 largely pale grey pollinose, with large reddish-brown sublateral spots and ventro-lateral areas, with a narrow median dorsal yellowish pollinose line. T4 and T5 without median discal setae, median marginal setae of T4 strong and erect. Measurements: body length 6.4 mm, wing length 5.9 mm [1 specimen].

Affinities

The name *intermedia* (used by Malloch as a manuscript name and adopted here) is appropriate for this species since some of its characters (particularly the lobate hind tibia and bristling of the posterior abdominal tergites) are those of *P. respondens* and its allies, but others (particularly the densely fringed paralobes) suggest some affinity with *P. buxtoni* or *P. hirtimana*. On balance most characters (especially the hypopygium) indicate affinity with *P. buxtoni*.

Material examined

Holotype ♂, PHILIPPINE ISLANDS: Luzon Baguio, — (Baker). In the United States National Museum, Washington. Paratype ♀, same data as holotype (U.S. Nat.Mus.). [Both holotype and paratype have, on their labels, between the words Baguio and Baker a word which appears to be "Benguet". The meaning of this word is not clear.]

Distribution

Known only from the type material from the Philippines.

Pygophora hirtimana Malloch, 1935

Pygophora hirtimana Malloch, 1935, *Proc. Linn. Soc. N.S.W.* 60: 77. Holotype ♂, NEW BRITAIN. Holotype lost, formerly in the School of Public Health and Tropical Medicine, Sydney.

Diagnosis

♂. Hind tarsus with the third segment produced poster-dorsally into a lobe bearing a long dense fringe of hairs (Fig. 24), mid tibia with a shallow antero-ventral notch (Fig. 20), hind tibia with a row of several strictly *p* setae along its length and with a few strictly *a* setae, paralobes of hypopygium with a short dense fringe of hairs postero-basally.

Description

♂. *Head*: occiput yellowish-grey pollinose. Interfrontal area deep brownish-yellow or orange-yellow, darker towards the ocellar triangle. Face, parafacials and parafrontals pale yellow pollinose. Ocellar setae fine but longer than the upper reclinate frontal setae which are short but rather strong. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae bright orange-yellow, third segment about 3.6 times as long as second segment and falling short of mouth-margin by about two-fifths of its length; arista long-plumose on basal half. Palpi yellow. Mentum dark yellowish-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and dorsum densely grey pollinose, mesonotum without

vittae. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a very weak *dc* setula; two well developed *post ia* setae present. *Wings*: hyaline or with a very faint yellowish tinge. Calyptrae pale yellowish with yellowish-white fringes. Halteres pale yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with the *pv* seta long, only a little shorter than the distance from its insertion to apex of tibia, and with two *ad* setae. Mid coxa with the paired ventro-apical setae very strong and closely applied to one another; mid femur with two preapical *p* setae, with a row of several strong *av* setae (cf. *P. buxtoni*), posterior surface (Fig. 11) with four strong submedian *pv* setae which are followed by fine setae and a row of very strong close-set setae lying a little dorsal to the *pv* edge, these setae in turn followed by a bare area and a few very small setulae at the apex; mid tibia with a shallow *av* notch (Fig. 20) near the base which gives the tibia a slightly twisted appearance, hairs of the ventral surface rather dense beyond the notch, without an *ad* seta, the two *pd* setae one and two times as long as tibial diameter. Hind femur on posterior surface near the base with an area of short stubby black setae (similar to those in *P. buxtoni*, Fig. 27) and with only one long submedian *pv* seta; hind tibia (Fig. 15) rather short, without a preapical lobe or *pv* setae but with a row of several well developed *p* setae along its length, with a few strictly *a* setae, and with several small *ad* setae in addition to the normal two *ad* setae, the second *ad* and second *pd* setae and the *d* preapical seta very long, the *d* preapical seta much longer than the hind metatarsus which is shorter than usual; hind tarsus with the third segment developed into a rounded postero-dorsal lobe which bears a dense inwardly-directed fringe of hairs (Fig. 24), fourth segment with a shorter fringe of hairs and second segment with a series of strong spinous *pv* setae. All claws with unusually long fringe hairs. *Abdomen* (Fig. 57): subcylindrical in form, slightly laterally compressed towards the apex but T5 not produced dorsally into a flattened keel although in lateral view it stands slightly higher than T7 + 8, lobes of sternite 5 of medium size and more or less rounded. Tergites pale testaceous yellowish basally becoming more pale orange-yellowish apically with pale yellowish-white pollinosity but only with indistinct spots; T1 + 2 without trace of darker colouring, T3, T4 and T5 each with yellowish or pale brownish-yellow median and sublateral spots (sometimes more or less absent from T3), T7 + 8 with a faint median dorsal yellowish spot but without trace of sublateral spots; epandrium yellowish. Venter pale testaceous yellow, lobes of sternite 5 semi-translucent yellow, paralobes of hypopygium yellow. T3 with the pair of dorso-lateral setae weak or absent (cf. *P. buxtoni*), tergites without specialised bristling but ventro-apical marginal setae of T5 long and strong, and T7 + 8 postero-ventrally with two or three strong bristly hairs near the base of the epandrium on either side. Hypopygium as in Fig. 96, each paralobe posteriorly near the base with a short dense black fringe of hairs and with the apical margin densely fringed with short curved hairs. *Measurements*: body length 6.6 mm (range 6.4 to 7.0 mm), wing length 5.9 mm (range 5.6 to 6.2 mm) [4 specimens].

♀. Closely similar to the ♀ of *P. buxtoni* but the spots of abdominal T3 more distinctly separated in the single (teneral) specimen seen. The ♀ lacks the ♂ secondary characters of fringed hind tarsus, grooved mid tibia, *p* and *a* setae and supernumerary *ad* setae of hind tibia, and specialised bristling of *p* surface of hind femur and

mid femur; hind femur with three very long equal *pv* setae in basal half. T4 and T5 without median discal setae. Measurements: approximately as ♂, only one teneral fly with damaged wings seen.

Affinities

P. hirtimana (♂) is the most easily recognised species of *Pygophora* with several remarkable specialised characters in the legs, particularly the fringed hind tarsus (from which its name is derived) and the curious shallow notch at the base of the mid tibia; the general form and the characteristic structure of the ♂ genitalia indicate close affinity with *P. ctenophora* Bezzi from Fiji and with *P. buxtoni* from Samoa (which, although occurring in Polynesia, has without doubt been derived from Melanesian forms).

Material examined

BISMARCK ARCHIPELAGO (Territory of New Guinea): 1 ♂, Admiralty Islands, Manus, 28.viii.1932 (*J. L. Froggatt*); 1 ♂, Admiralty Islands, Manus, 1932 (*N. E. H. Caldwell*). SOLOMON ISLANDS: 2 ♂♂, Russell Island, Somata, 22.ii.1934 (*R. A. Lever*), 1 ♂, Guadalcanal, Lunga, vii.1933 (*R. J. A. W. Lever*); 1 ♂, Tulagi, 9.ii.1935 (*R. A. Lever*); 1 ♂, 1♀, Rennell Island, Niupani, 22.xi.1953 (*J. D. Bradley*). All material in B.M.Nat.Hist.

The ♂ holotype of *P. hirtimana* (NEW BRITAIN: Rabaul (*F. H. Taylor*)) is lost. It was formerly in the School of Public Health and Tropical Medicine at Sydney, but Mr. D. J. Lee informs me that careful search there and also in the U.S.Nat.Mus. and Malloch's collection have failed to trace it. *P. hirtimana* is however an unmistakable species (the unique hind tarsus was figured by Malloch with the original description) which is very unlikely to be confused with any other, and I have therefore not designated a neotype.

Distribution

A Melanesian species occurring so far as is known only in the Bismarck Archipelago and the Solomon Islands.

Pygophora ctenophora Bezzi, 1928

Pygophora ctenophora Bezzi, 1928, *Dipt. Brach. Ath. Fiji Is.*: 169. Holotype ♂, FIJI ISLANDS. In the British Museum (Natural History), London.

Diagnosis

♂. Abdomen with sides of T4 completely bare and sides of T5 with areas of dense fine hairs, closely matted together (Fig. 58); mid femur with a short double row of *pv* setae in apical third followed by a bare area (similar to *hirtimana*, Fig. 11); paralobes of hypopygium each with a dense black fringe of hair postero-basally.

Description

♂. *Head*: occiput densely pale grey pollinose, the pollinosity pale yellowish anteriorly against the eye-margins. Interfrontal area deep yellow. Face, parafacials and parafrontals golden-yellow pollinose. Ocellar setae well developed, about equal in length to upper reclinate frontal setae but finer. Parafrontals

without supernumerary setae between upper and lower inclinate setae. Antennae bright yellow-orange, third segment about 4.0 times as long as second segment and falling short of mouth-margin by nearly one-third of its length; arista long-plumose on basal half. Palpi yellowish-white. Mentum dark yellowish-brown or red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely grey pollinose, dorsum yellowish-grey pollinose without trace of vittae. Presutural acrostichal hairs in two rows; no distinct *dc* setula developed in front of the *prst dc* seta; two *post ia* setae present. *Wings*: with a very faint yellowish tinge. Calyptrae white with white fringes. Halteres pale creamy-yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with two small *ad* setae, the *pv* seta long and fine and about three-quarters as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, *pv* surface with three or four setae in basal two-thirds and in the apical third with a double row of strong setae followed by a bare area and a few small setulae at the apex (generally similar to *P. hirtimana*, Fig. 11); mid tibia with a very slight trace of an emargination ventrally near the base followed by an area of rather dense ventral hairs, without an *ad* seta, the two *pd* setae unusually short with the first one only about half as long as the tibial width and the second one subequal in length to the tibial diameter. [Hind legs missing in all material seen, but hind tibia without a preapical lobe (Bezzi, original description) and with second *ad* and second *pd* setae very long—described by Bezzi as “two very long bristles in middle”.] *Abdomen* (Fig. 58): broad basally but in dorsal view strongly contracting behind, strongly laterally compressed medio-ventrally (T4 and T5), but T5 not forming a dorsal keel, lateral lobes of sternite 5 large and subtriangular. T1 + 2 and T3 entirely pale testaceous yellowish with very pale hind margins; T4 mainly yellowish or pale reddish-yellow with paler hind margin and with large orange-brown or blackish-brown median and sublateral spots, the spots separated by distinct grey or yellowish pollinose areas; T5 pale orange-yellow or reddish-yellow, especially laterally, dorsally slightly darkened in ground colour with dense greyish-yellow or pale yellow pollinosity and with large distinct reddish-brown or black-brown median and sublateral spots, hind margin narrowly pale reddish-yellow; T7 + 8 mainly yellowish-orange or dark greyish in ground colour with yellowish or greyish-yellow pollinosity and an indistinct pair of small brownish sublateral spots, dorsal apex also somewhat brownish; epandrium reddish or deep yellowish-orange. Venter yellowish, lobes of sternite 5 pale translucent yellow, paralobes of hypopygium reddish-yellow. Sides of T4 bare, devoid of the usual hairs; T5 on each side with a large area of fine dense hairs which are slightly curled and matted together, ventro-apical marginal setae very regularly inserted and subequal in length, hind margin of the tergite between the ventro-apical setae and the dorsal median marginal setae without marginal setae. Hypopygium as in Fig. 95, each paralobe postero-basally with a very dense black fringe of hairs and along most of the posterior margin with a short fringe of close-set curled hairs. *Measurements*: body length 6.2, 6.3 mm, wing length 5.9, 5.8 mm [2 specimens].

♀. Antennae shorter than in ♂, interfrontal area dark orange ventrally becoming more reddish towards ocellar triangle, mid femur without the specialised bristling of the ♂ and mid tibia without trace of emargination near the base. Abdomen

normal, T1 + 2 entirely pale orange-yellow, T3 mainly yellowish-orange but with bold dark brown median and sublateral spots (the latter more or less rounded) which are connected by dark areas covered with grey pollinosity and laterally with traces of narrow brownish bands extending towards the ventral surface, T4 yellowish-orange basally and apically and medially with a broad band of dark ground colour with grey pollinosity and distinct blackish-brown median and sublateral spots, T5 entirely dark with dense grey pollinosity and a well marked pair of blackish-brown sublateral spots but no median spot. T4 and T5 without median discal setae. Measurements: body length 6.7 mm, wing length 6.4 mm [1 specimen].

Affinities

P. ctenophora is clearly allied to *P. hirtimana* Malloch and *P. buxtoni* Malloch, the three species having a closely similar type of ♂ genitalia and mid femoral bristling; the ♂ shows a very slight trace of the ventral basal emargination of the mid femur which, in more developed form, is a characteristic of *P. hirtimana*. Unfortunately the hind legs are missing from the males examined (the only material known), and Bezzi's original description includes nothing on the hind femora, but the hind femora probably possess the curious short stubby setae near the base on the posterior surface which is characteristic of both *hirtimana* and *buxtoni*.

Material examined

Holotype ♂, FIJI ISLANDS: Natova, v.1918 (*R. Veitch*). Paratype ♂, FIJI ISLANDS: Nasese, 31.vii.1921 (*H. W. Simmond*) (B.M.Nat.Hist.) and paratype ♀, FIJI ISLANDS: Ovalau, v.1921 (*H. W. Simmond*) (B.M.Nat.Hist.). FIJI ISLANDS: 1 ♂, Natova, iv.1918 (*R. Veitch*) (B.M.Nat.Hist.); 1 ♀, Lau Group, Oneata, 19.viii.1924 (*E. H. Bryan*) (Bishop Mus.); 1 ♀, Lau Group, Namuka, 12.viii.1924 (*E. H. Bryan*) (Bishop Mus.); 1 ♀, Gau Group, Navutu-i-Loma, 8.viii.1924 (*E. H. Bryan*) (Bishop Mus.); 1 ♀, Viti Levu, Lami, iii.1951 (*N. L. H. Krauss*) (Bishop Mus.).

Distribution

Known only from the above-listed material from the Fiji Islands and perhaps an endemic species confined to this group. *P. ctenophora* is recorded and keyed out by Emden (1942) in his paper on the Coenosiinae of Fiji.

Pygophora buxtoni Malloch, 1929

Pygophora buxtoni Malloch, 1929, *Insects of Samoa* pt. 6, 3: 160. Holotype ♂, SAMOA. In the Bernice P. Bishop Museum, Honolulu.

Diagnosis

♂. With the *pd* setae of mid tibia extremely long and fine, inserted at a right-angle to the tibia and equal in length (Fig. 22); hind femur with an area of short blunt spinous setae on posterior surface near the base; hind tibia with the *d* pre-apical seta and the second *ad* seta extremely long, fine and slightly sinuous, the *pd* surface with two fine setae in addition to the normal two *pd* setae (Fig. 16); paralobes of hypopygium each with a large rounded postero-basal lobe bearing a fringe of very long bristly hairs (Fig. 97).

Description

♂. *Head*: occiput densely silvery-grey pollinose. Interfrontal area bright reddish-orange. Face bright yellow pollinose, parafacials and parafrontals golden-yellow pollinose. Ocellar setae fine, a little longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange-yellow, third segment about 4.0 times as long as second segment and falling short of mouth-margin by about one third of its length; arista long-plumose on basal half. Palpi yellow. Mentum orange-brown. *Thorax*: entirely reddish-black in ground colour, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and dorsum densely grey pollinose, mesonotum with distinct brown vittae, a median *acr* vitta and a pair of *dc* vittae. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a very weakly differentiated *dc* setula; two strong *post ia* setae present. *Wings*: very faintly smoky brownish, most definitely darkened anteriorly on apical half. Calyptrae very pale yellowish-white with yellowish-white fringes. Halteres yellow. *Legs*: rather longer than usual with distinctly elongate femora and tibiae, colour entirely yellow (including the coxae). Fore tibia with the *pv* seta very long and sinuous, about equal in length to distance from its insertion to apex of tibia, and with two or three small rather indistinct *ad* setae. Mid coxa with the paired ventro-apical setae very long; mid femur with two preapical *p* setae, *av* surface with one very long strong submedian seta, *pv* surface with three long strong setae in basal two-thirds followed by a short double series of close-set setae and a bare area, with a few very small *pv* setulae at the apex (similar to *P. hirtimana*, Fig. 11, but the setae of the doubled row finer); mid tibia without an *ad* seta, the two *pd* setae very long and fine, about five times as long as tibial diameter and standing out at right-angles to the tibia, the second of the two inserted almost exactly at the middle of the tibia and the more basal seta inserted unusually near to the base. Hind femur on posterior surface near the base with an area of short blunt black spinous setae and with two long subequal submedian *pv* setae (Fig. 27); hind tibia without a preapical lobe or *pv* setae, but with two or three fine *p* setae in apical half and with two *pd* setae in addition to the normal two *pd* setae, the second *ad* seta and the *d* preapical seta exceedingly long and fine and slightly sinuous (Fig. 16), the *d* preapical seta distinctly longer than hind metatarsus; hind tarsus simple. *Abdomen*: very slightly laterally compressed but T5 not forming a flattened dorsal keel although in lateral view it is slightly higher than T7 + 8 (as in *P. hirtimana*, Fig. 57), lateral lobes of sternite 5 small and rounded. T1 + 2 and T3 yellow, T4 yellow with reddish-brown median and sublateral spots which are narrowly joined by darkish areas with pale greyish pollinosity; T5 yellowish ventro-laterally and dorsally on anterior margin, rest of dorsum dark in ground colour with brown median and sublateral spots which are separated by pale grey pollinose areas; T7 + 8 mainly dark in ground colour with pale grey pollinosity and a pair of small dark brown sublateral spots. Venter, lobes of sternite 5 and paralobes of hypopygium yellowish. The pair of dorso-lateral setae of T3 very long and strong, median marginal setae of T5 very strong, the ventro-apical marginal setae of T5 very long and fine. Paralobe of hypopygium as in Fig. 97, with a broad rounded postero-basal lobe bearing a dense fringe of very long sinuous bristly

hairs. *Measurements*: body length 7.2 mm, wing length 6.9 mm [1 specimen].

♀. Similar to ♂ with brownish-tinged wings but antennae shorter, mesonotal vittae more distinct with the *dc* vittae almost blackish, and legs without the secondary characters of the ♂ (mid femur without the doubled row of *pv* setae and with three long *pv* setae, mid tibia with the *pd* setae normal although the more basal one is inserted closer to the base than in most species, hind femur without the area of short stubby setae on the posterior surface and with three *pv* setae, hind tibia without *p* setae or supernumerary *pd* setae and the second *ad* seta and the *d* preapical seta less fine and sinuous). Abdomen with T1 + 2 and most of T3 pale yellowish-orange, T3 dorsally with a large transverse dark reddish-brown mark formed of coalesced median and sublateral spots, the separation between the spots being very faintly indicated by narrow traces of thin whitish pollinosity; T4 pale yellowish-orange basally and apically, with bold dark brown median and sublateral spots which are separated by grey pollinose areas, the sublateral spots extending round laterally to the ventral surface; T5 mainly grey with a pair of large bold dark brown sublateral spots but no trace of a median spot, only narrowly pale yellowish-orange basally. T4 and T5 without median discal setae. *Measurements*: body length 7.4, 6.5 mm, wing length 6.6, 6.0 mm [2 specimens].

Affinities

P. buxtoni is closely allied to *P. ctenophora* Bezzi and *P. hirtimana* Malloch, all three species showing a generally closely similar hypopygium. The form and bristling of the ♂ abdomen suggests, however, closer affinity with *hirtimana* than *ctenophora*. The curious long fine subequal *pd* setae of the mid tibia distinguish *buxtoni* ♂ from all other *Pygophora*, and even in the ♀ the more basal of the two mid tibial *pd* setae is inserted closer to the base than in other species.

Material examined

Paratype ♂, SAMOA: Tutuila, Pago Pago, 19.iv.1924 (*E. H. Bryan*) (U.S.Nat. Mus.); paratype ♀, SAMOA: Tutuila, Pago Pago, 18.iv.1924 (*E. H. Bryan*) (Bishop Mus.); paratype ♀, SAMOA: Tutuila, Vaitogi, 23.ix.1923 (*Swezey and Wilder*) (B.M. Nat.Hist.); paratype ♀, SAMOA: Tutuila, Afono Trail, 25.ix.1923 (*Swezey and Wilder*) (B.M.Nat.Hist.); paratype ♀, SAMOA: Tutuila iv.1918 (*E. C. Kellers*) (Bishop Mus.).

I have not seen the holotype of this species (Bishop Mus.), but the data is the same as that given above for the ♂ paratype from Pago Pago.

Distribution

Known only from the island of Tutuila in the Samoa group.

Pygophora trimaculata Karl, 1935

Pygophora trimaculata Karl, 1935. *Arb. morph. taxon. Ent. Berl.* 2: 48. Lectotype ♂, FORMOSA. In the Deutsches Entomologisches Institut, Berlin.

Lectotype designation: Karl described *P. trimaculata* from four syntypes (2♂, 2♀) (D.Ent.Inst.). One ♂ has been selected and labelled as lectotype, and the other

♂ has been labelled paralectotype. The two ♀ syntypes are probably not conspecific with the lectotype.

Diagnosis

Parafrontals with a supernumerary pair of inclinate frontal setae between the upper and lower pairs of inclinate frontal setae (Fig. 7), extreme bases of femora brown, ♂ antennae very elongate, lateral lobe of sternite 5 bifurcate with the upper branch truncate, paralobe of hypopygium shaped as in Fig. 99.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area dark velvety reddish-orange. Face and parafacials densely white pollinose, parafrontals pale golden-yellow pollinose. Ocellar setae strong, about equal in length to but finer than lower reclinate frontal setae. Parafrontals with a pair of strong supernumerary inclinate setae between the upper and lower pairs of inclinate frontal setae. Antennae brownish-yellow basally, third segment orange and very elongate, about 6 times as long as second and almost reaching mouth-margin (only falling short by about one-thirteenth of its length); arista long-plumose on basal two-fifths, the plumose hairs shorter than usual. Palpi pale yellow. Mentum dark yellowish-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely pale grey pollinose, mesonotum pale yellowish pollinose with distinct darker yellow-brown pollinose vittae, a narrow median *acr* vitta and a pair of more diffuse broader *dc* vittae. Presutural acrostichal hairs in two rows, the hindmost pair of presutural acrostichals developed as strong setae; *prst dc* seta preceded by a distinctly differentiated *dc* setula; two well developed *post ia* setae present. *Wings*: entirely hyaline. Calyptrae yellowish-white with white fringes. Halteres pale creamy-yellow. *Legs*: almost entirely orange-yellow but extreme bases of all femora pale red-brown or brown (fore femora more distinctly darkened basally than other femora), coxae reddish or reddish-grey with pale grey pollinosity. Fore tibia with the *pv* seta short and fine, only half as long as distance from its insertion to apex of tibia, and with two or three very small *ad* setae. Mid femur with two preapical *p* setae, without specialised bristling, with three short and very fine *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the two *pd* setae one and a half and two times as long as tibial diameter. Hind femur with a very long submedian *pv* seta and a smaller *pv* seta on either side of it; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about two-thirds as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 73): deep in lateral view but only very slightly compressed latero-ventrally, in dorsal view T5 abbreviated and much shorter than the other tergites, abdomen in dorsal view appearing only very slightly constricted between T5 and T7 + 8, lateral lobes of sternite 5 more or less bifurcate with the upper arm truncate (Fig. 118). All tergites dark in ground colour (except for the exceedingly narrow pale hind margins) and pale grey pollinose so that abdomen is predominantly grey (somewhat silvery-grey latero-ventrally); T3, T4 and T5 each with a large bold black pair of sublateral spots and each with a large subtriangular dark golden-brown pollinose median spot, T1 + 2 with a trace of a median golden-brown

pollinose area but otherwise not darkened, T7 + 8 with only a trace of small blackish sublateral spots visible in certain lights and with some indistinct yellowish-brown pollinosity dorsally; epandrium dark brownish-orange with thin pale yellowish-grey pollinosity especially towards the base. General abdominal pattern similar to *P. keiseri*, Fig. 36. Venter silvery-grey except for hind margins of sternites which are pale yellow, lateral lobes of sternite 5 translucent reddish-yellow, paralobes of hypopygium shining reddish-yellow. Tergites without specialised bristling, but setae of T7 + 8 rather strong and numerous, ventro-apical marginal setae of T5 weak, long but very fine. Hypopygium with paralobes shaped as in Fig. 99, each paralobe antero-ventrally with long bristly hairs (absent in *P. keiseri*) and with a few very short blunt black spinules posteriorly at the apex. *Measurements*: body length 6.4 mm, wing length 5.8 mm [1 specimen].

♀. Not definitely known as the ♀ syntypes are almost certainly not correctly associated with the ♂. Female probably closely similar to that of *P. keiseri*, with partly darkened femora, supernumerary parafrontal setae, and all grey abdomen with large black spots.

Affinities

Closely allied to *P. keiseri* sp. n. and *P. floresana* (Hennig), but ♂ distinguished from both these species by the truncate upper arm of the lateral lobe of sternite 5 and by the shape of the paralobes.

Material examined

Lectotype ♂, FORMOSA: Tainan, iv.1910 (*Sauter*); paralectotype ♂, data as for lectotype.

In addition to this material I have seen the two ♀ syntypes from Formosa; these disagree with the males in several important respects and it is very unlikely that the females are conspecific with the males. The females lack the extra pair of inclinate frontal setae and the femora are entirely yellow (if the femora are at all darkened in the males of *Pygophora* they are more extensively darkened still in the females); furthermore the abdomen is partly yellowish basally and the fore coxae are yellow, and the abdominal spots do not closely resemble those of *P. keiseri* as should be likely in view of the very close affinity shown by the males. The pattern of the abdomen and yellow fore coxae and general colouring (e.g. the absence of the yellowish-brown mesonotal vittae) all serve to place the females somewhere near *P. macularis* (Wiedemann) and it is possible that they are in fact females of *P. maculipennis* Stein, which is extremely closely related to *macularis* and which appears to be common in Formosa (*macularis* is not known from Formosa); but it is more likely that the ♀ of *maculipennis* has dark femora and that the ♀ syntypes of *trimaculata* belong to another species altogether, neither *trimaculata* nor *maculipennis*.

Distribution

Known only from Formosa.

Pygophora floresana (Hennig, 1952) **comb. n.**

Lispocephala floresana Hennig, 1952, *Beitr. Ent.* 2: 70. Holotype ♂, FLORES. In the Deutsches Entomologisches Institut, Berlin.

Diagnosis

Parafrontals with a pair of supernumerary setae between upper and lower pairs of inclinate frontal setae and all femora blackish-brown on basal two-thirds or three-quarters in both sexes; ♂ sternite 5 with lateral lobes bifurcate and paralobes of hypopygium as in Fig. 74.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area deep orange-reddish. Face and parafacials pale greyish-yellow pollinose, parafrontals pale yellow pollinose. [Ocellar setae missing from holotype, probably strong and much longer than upper reclinate frontal setae.] Parafrontals with a pair of supernumerary setae between upper and lower pairs of inclinate frontal setae [all frontal setae missing from holotype but presence of supernumerary setae evident from the pores]. Antennae yellow-orange, third segment very elongate, 5 times as long as second segment and falling short of mouth-margin by only about one-eighth of its length; arista long-plumose on basal two-fifths. Palpi yellow. Mentum dark red-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and most of dorsum grey pollinose, mesonotum with distinct darker yellow-brown pollinose vittae, a narrow median *acr* vitta and broader *dc* vittae. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a distinctly differentiated *dc* setula [the setulae missing from holotype but the pores evident]; two *post ia* setae present. *Wings*: entirely hyaline. Calyptrae white with white fringes. Halteres yellow. *Legs*: coxae reddish or reddish-black with pale grey pollinosity, all femora blackish-brown on basal two-thirds (mid femora) or three-quarters (fore and hind femora), apices of femora, tibiae and tarsi yellow. Fore tibia with the *pv* seta short and fine, about half as long as distance from its insertion to apex of tibia, and with two or three very small *ad* setae. Mid femur with two preapical *p* setae, without specialised bristling, with three long *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the two *pd* setae one and two times as long as tibial diameter. Hind femur with a very long submedian *pv* seta and with a slightly shorter *pv* seta on either side of it; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta long and about three-quarters as long as hind metatarsus; hind tarsus simple. *Abdomen* [missing from holotype but hypopygium slide-mounted]: probably shaped much as in *P. keiseri* (Fig. 36), lateral lobe of sternite 5 bifurcate with the upper arm acuminate. Abdomen predominantly grey, dark in ground colour with pale grey pollinosity, tergites with indistinct median and sublateral spots, the median spots more or less forming a median line [original description]. Lateral lobes of sternite 5 translucent yellow, paralobes of hypopygium shining reddish-yellow. Tergites without specialised bristling. Hypopygium as in Fig. 74. *Measurements*: body length (estimated) 5.25 mm, wing length 4.6 mm [1 specimen].

♀. Generally similar to ♂, but antennae of normal length with third segment

brown except at extreme base and basal segments brownish, interfrontal area dark brick-red, and wings with a yellow tinge anteriorly. Abdomen grey, dark in ground colour with pale grey pollinosity (extreme hind margins of T1 + 2, T3 and T4 pale yellowish), T3 and T4 with bold brownish-black median and sublateral spots, T5 with blackish sublateral spots and a median yellowish-brown pollinose line, T1 + 2 slightly darkened basally. T4 without median discal setae, T5 with irregular median discal setae. Measurements: body length 6.4 mm, wing length 5.8 mm [1 specimen].

Affinities

P. floresana is very closely allied to *P. keiseri* sp. n. but differs chiefly in the ♂ hypopygium in which the paralobes are very differently shaped. The females of the two species are very alike and the characters given in the key for their separation may not be constant. *P. floresana* is also closely allied to *P. trimaculata* Karl but is smaller and the upper arm of the bifurcate lateral lobe of the ♂ sternite 5 is acuminate instead of truncate.

Material examined

Holotype ♂, FLORES (Indonesia): Rana Mesé, 20–30.vi.1927 (*Sunda Expedition*). Paratype ♀, locality as for holotype, 22.vi.1927 (*Sunda Expedition*) (D.Ent.Inst.).

Distribution

Known only from the type material from the western part of Flores island, Indonesia.

***Pygophora keiseri* sp. n.**

Diagnosis

Parafrontals with a pair of supernumerary setae between upper and lower pairs of inclinate frontal setae (Fig. 7), bases of femora blackish-brown, abdomen grey with bold black-brown spots (♂ as in Fig. 36), ♂ sternite 5 as in Fig. 117, paralobes of hypopygium as in Fig. 98, and antennae extremely elongate.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area deep yellow-orange anteriorly and dark reddish posteriorly or all brownish-yellow. Face and para-facials densely silvery-white pollinose, parafrontals pale yellow pollinose. Ocellar setae very strong, longer than upper reclinate frontal setae. Parafrontals with a pair (sometimes on one side only) of supernumerary inclinate setae between upper and lower pairs of inclinate frontal setae (Fig. 7). Antennae with first two segments brownish-yellow or pale brown, third segment pale yellowish-orange and very elongate, about 6.8 times as long as second segment and almost reaching the mouth-margin (falling short only by about one-twelfth of its length); arista long-plumose on basal two-fifths, the plumose hairs rather shorter than usual. Palpi yellowish-white. Mentum dark brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely pale grey pollinose, mesonotum grey or yellowish-grey pollinose with three distinct yellowish-brown pollinose vittae, a narrow median *acr* vitta and a pair of broader

more diffuse *dc* vittae. Presutural acrostichal hairs in two close-set rows; *prst dc* seta preceded by a clearly differentiated small *dc* setula; two *post ia* setae present. *Wings*: entirely hyaline. Calyptrae creamy-white with white fringes. Halteres pale creamy-yellow. *Legs*: coxae reddish-grey or blackish with pale grey pollinosity, femora dark brown or blackish brown basally, fore femora dark on basal third or half, mid and hind femora dark at least at base but usually on basal two-fifths or half; femora apically, tibiae and tarsi yellow. Fore tibia with the *pv* seta short and fine, only half as long as distance from its insertion to apex of tibia, and with two small *ad* setae. Mid femur with two preapical *p* setae, without specialised bristling, with four subequal *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the two *pd* setae short and only one and one and three-quarter times as long as tibial diameter. Hind femur with one very long submedian *pv* seta and a smaller *pv* seta on either side of it; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about three-quarters as long as hind metatarsus; hind tarsus simple. *Abdomen*: slightly laterally compressed towards the apex and deep in lateral view, in dorsal view slightly pinched in between T5 and T7 + 8 but T5 not formed dorsally into a flattened keel, lateral lobes of sternite 5 excavated on apical margins so that each lobe is more or less bifurcate with the upper lobe strongly produced and acuminate (Fig. 117). All tergites dark in ground colour (except for narrow pale yellowish hind margins of T1 + 2, T3 and T4) and pale grey pollinose so that abdomen is predominantly grey, T3, T4, T5 and T7 + 8 each with large bold dark blackish-brown or black median and sublateral spots (Fig. 36), T1 + 2 indistinctly darkened medially; epandrium dark brown with pale grey pollinosity. Venter greyish (margins of sternites pale), lateral lobes of sternite 5 semi-translucent yellow, paralobes of hypopygium semi-shining reddish-yellow. Tergites without specialised bristling, ventro-apical marginal setae of T5 weak (as in *P. trimaculata*, Fig. 73). Hypopygium as in Fig. 98, paralobes with abundant minute hairs and each at the apex of the inner surface with a few very small blunt black spinules. *Measurements*: body length 5.25, 5.5 mm, wing length 4.8, 5.0 mm [2 specimens].

♀. Generally similar to ♂, but antennae of normal length and slightly brownish towards the apices and the mesonotal vittae more distinct; interfrontal area usually deep velvety orange. Abdomen predominantly grey, dark in ground colour with pale grey pollinosity (only extreme hind margins of T1 + 2, T3 and T4 pale), T3 and T4 with bold black or blackish-brown median and sublateral spots, T5 with blackish sublateral spots but without definite median spot although the median area is distinctly yellowish-brown pollinose, T1 + 2 indefinitely darkened on basal half. T4 without median discal setae, T5 with a pair or with several irregular weak median discal setae. *Measurements*: body length 6.0 mm (range 5.6 to 6.5 mm), wing length 5.6 mm (range 5.2 to 6.0 mm) [4 specimens].

Affinities

P. keiseri is very closely related to *P. trimaculata* Karl and *P. floresana* (Hennig) but in the ♂ can be distinguished from both these species by the form of the paralobes of the hypopygium. The lateral lobes of sternite 5 are closely similar to those in *floresana*, but the upper prolongation of the lateral lobe is strongly pointed

whereas it is truncate in *trimaculata*. These three species form a distinctive group of species in which the femora of both sexes are partly dark, the parafrontals have a supernumerary pair of setae, the abdomen is more or less grey with bold blackish spots, and the lateral lobe of sternite 5 of the male is bifurcate.

Material examined

Holotype ♂, CEYLON: Central Province, Kandy, 3.ii.1954 (*F. Keiser*). In the Naturhistorisches Museum, Basel. Paratypes: 1 ♂, CEYLON: Central Province, Kandy, 3.ii.1954 (*F. Keiser*) (B.M.Nat.Hist.); 1 ♀, CEYLON: Central Province, Kandy, Roseneath, 29.ix.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♀, CEYLON: Central Province, Peradeniya, Experiment Station, 4.xi.1953 (*F. Keiser*) (Nat.Mus.Basel); 1 ♂, 5 ♀♀, S. INDIA: Nilgiri Hills, Cherangode, 3500 ft., x.1950 (*P. S. Nathan*) (B.M.Nat.Hist.); 1 ♀, S. INDIA: S. Coorg, Ammatti, 3100 ft., xi.1952 (*P. S. Nathan*) (B.M.Nat.Hist.).

Distribution

At present known only from the material listed above from Ceylon and southern India.

***Pygophora cheesmanae* sp. n.**

Diagnosis

♂. Distinguished by the structure of the postabdomen, the epandrium distinctly set off from T7 + 8, sternite 5 as in Fig. 124, hypopygium as in Fig. 66; parafrontals with a strong pair of supernumerary inclinate setae between the normal pairs of upper and lower inclinate frontal setae.

Description

♂. *Head*: occiput grey pollinose. Interfrontal area deep orange-yellow, slightly reddish towards ocellar triangle. Face and parafacials pale yellow pollinose, parafrontals yellow pollinose. Ocellar setae well developed, a little longer than upper reclinate frontal setae. Parafrontals with one pair of strong supernumerary setae between upper and lower pairs of inclinate frontal setae, so that there are three pairs of inclinate frontal setae altogether. Antennae orange, third segment about 3.1 times as long as second segment and falling short of mouth-margin by about one-third of its length; arista plumose on basal third, hairs a little shorter than in most species. Palpi yellowish-white. Mentum pale red-brown or yellow-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae, mesonotum and scutellum grey pollinose, mesonotum with distinct traces of yellowish-brown or brown median and dorsocentral vittae. Presutural acrostichal hairs in two close rows; no *dc* setula preceding the *prst dc* seta; two strong *post ia* setae present. *Wings*: apical third with indefinite smoky brown suffusion which is more intense towards anterior margin, otherwise more or less hyaline. Calyptrae white with white fringes. Halteres creamy-white. *Legs*: entirely yellow except for mid and hind coxae which are reddish-black with grey pollinosity. Fore tibia without distinct *ad* setae although a few small setulae are usually distinguishable, the *pv* seta short and only about three-fifths as long as distance from its insertion to apex of tibia. Mid coxa with numerous but rather

weak ventro-apical setae; mid femur with two preapical *p* setae, without specialised bristling, with the usual three long fine *pv* setae and a smaller seta near the base; mid tibia without an *ad* seta, the two *pd* setae about two and three and a half times as long as tibial diameter. Hind femur with three long *pv* setae in basal three-fifths; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about three-quarters as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 65): of unusual form with epandrium (T9) distinctly set off from T7 + 8, sternite 5 very enlarged and shaped as in Fig. 124, in the holotype the lateral lobes are infolded in the horizontal plane and overlap in the mid-line (Fig. 40). All tergites dark in ground colour with grey pollinosity, only the hind margins of T1 + 2, T3 and T4 narrowly yellowish; T3, T4 and T5 with distinct blackish median and sublateral spots, the sublateral spots of T5 very distinct and rounded but those on T3 and T4 less defined laterally and extending on to sides of tergite; T5 with a pair of lateral spots in addition to sublateral spots which are distinct when seen from behind but very indistinct when seen laterally; T7 + 8 with small black-brown median and sublateral spots, much less distinct than those on preceding tergites. Venter, including sternite 5, blackish in ground colour with grey pollinosity, paralobes of hypopygium and apices of lobes of sternite 5 shining reddish-brown. T5 with a row of about eight very long ventro-apical setae on either side, but tergites without specialised bristling; epandrium with long fine hairs laterally on the ridge above the base of each paralobe, and usually with one pair of long setae apically. Hypopygium (Fig. 66) with very large clavate paralobes which are rounded on the outer edge and bear a setulose process on the anterior edge with a basal tuft of strong bristles, the paralobes slightly variable in shape on the antero-apical corner which is broadly rounded or strongly acuminate. *Measurements*: body length 6.2 mm (range 5.2 to 6.7 mm), wing length 5.6 mm (range 5.2 to 5.8 mm) [4 specimens].

♀. Generally like the ♂ with all yellow legs, but wings entirely hyaline in the single specimen seen and the three mesonotal vittae more boldly blackish-brown. Abdomen mainly dark in ground colour, only the sides of T1 + 2 and the hind margins of T3 and T4 narrowly yellowish; T1 + 2 mainly greyish pollinose with an indefinite median blackish area; T3, T4 and T5 each with large bold black median and sublateral spots, and traces of ventro-lateral spots, otherwise grey pollinose with a slightly greenish tinge in certain lights. T4 without median discal setae, T5 in the one ♀ seen with a median discal seta on one side of the median black spot (probably a strong pair of median discals normally present). *Measurements*: body length 6.4 mm, wing length 5.7 mm approximately [1 specimen].

Affinities

P. cheesmanae is closely allied to *P. villicoxa* sp. n. and *P. dolabra* sp. n., both of which are also from New Guinea. It is easily distinguished from *villicoxa* by the yellow-orange (instead of brown) antennae, by lacking the dense fringe of setae on the mid coxa, and by the detailed structure of the postabdomen. From *dolabra*, apart from genital characters, it is easily separated by the presence of a supernumerary pair of inclinate frontal setae.

Material examined

Holotype ♂, DUTCH NEW GUINEA: Japen Island, camp 2, Mt. Eiori, 2000 ft., x.1938 (*L. E. Cheesman*). In the British Museum (Natural History), London. Paratypes: 1 ♂, DUTCH NEW GUINEA: Wisselmeren, Itouda, Kamo Valley, 1500 m, 12.viii.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.); 1 ♂, DUTCH NEW GUINEA: Wamena, 1700 m, 10-25.ii.1960 (*T. C. Maa*) (Bishop Mus.); 1 ♂, DUTCH NEW GUINEA: Hittikima, 100 m, 19.ii.1960 (*T. C. Maa*) (Bishop Mus.); 1 ♂, N.E. NEW GUINEA: Moife, 15 km N.W. of Okapa, 2100 m, 7-14.x.1959 (*T. C. Maa*) (Bishop Mus.); 1 ♂, N.E. NEW GUINEA: Sepalakambang, Salawaket Range, 1920 m, 12.ix.1956 (*E. J. Ford*) (Bishop Mus.); 1 ♀, N.E. NEW GUINEA: Goroka-Kabebe, 1800 m, 24.vi.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.).

Distribution

Known only from the material listed above from New Guinea and probably confined to this territory.

Pygophora villicoxa* sp. n.Diagnosis*

♂. Mid coxa with an unusually dense fringe of ventro-apical setae (Fig. 25), mid and hind femora basally with long fine erect hair on ventral surface, abdomen as in Fig. 63. Both sexes with dark brown third antennal segment, reddish-brown interfrontal area, a pair of strong supernumerary inclinate frontal setae and a slightly flattened hind metatarsus.

Description

♂. *Head*: occiput pale greyish pollinose. Interfrontal area reddish-brown or dark orange-brown but darkened laterally so that it is slightly blackish along the parafrontal margins. Face pale greyish-yellow pollinose, parafacials dirty whitish-yellow pollinose over a yellowish ground colour, parafrontals and ocellar triangle pale yellowish pollinose over a blackish ground colour. Ocellar setae long and fine, much longer than upper reclinate frontal setae. Parafrontals with a strong pair of supernumerary inclinate setae between the upper and lower pairs of inclinate frontal setae so that there are three strong pairs of inclinate setae altogether, sometimes with a second additional seta or hair. Antennae dark reddish-brown basally, only slightly yellowish dorsally on second segment, third segment entirely dark brown or dark reddish-brown, third segment about 3 times as long as second segment and falling short of mouth-margin by about half its length; arista plumose on basal third, the hairs a little shorter than in most species. Palpi yellowish-white. Mentum reddish-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; dorsum dark grey pollinose, the mesonotum with three faint brownish pollinose vittae, areas between the vittae slightly brownish-grey pollinose. Presutural acrostichal hairs in two rows; without a *dc* setula preceding the *prst dc* seta; two well developed *post ia* setae present. *Wings*: entirely hyaline. Calyptrae whitish, upper calypter with slightly brownish margin, fringes yellowish-white. Halteres pale yellow. *Legs*: yellow, including the fore coxae, only mid and hind coxae reddish-black with grey pollinosity.

Fore tibia with one or two very small indistinct *ad* setulae, the *pv* seta fine and about three-quarters as long as distance from its insertion to apex of tibia. Mid coxa with unusually dense ventro-apical setae (Fig. 25); mid femur with two preapical *p* setae, with the usual three long *pv* setae in basal two-thirds and shorter finer setae nearer the apex, the ventral surface of the basal half with numerous long fine erect yellowish-brown hairs; mid tibia without an *ad* seta, the two *pd* setae about two and a half and three and a half times as long as tibial diameter. Hind femur with two long submedian *pv* setae and a smaller seta nearer the base, ventral surface with long fine erect hair on the basal half similar to that on mid femur; hind tibia without a preapical lobe or *pv* setae, the distal *ad* and distal *pd* setae very long, the *d* preapical seta shorter than these but about equal in length to hind metatarsus (which is rather short); hind metatarsus slightly flattened laterally. *Abdomen* (Fig. 63): short, broad and deep, with very large oval lateral lobes to sternite 5, epandrium very distinctly set off from T7 + 8. T1 + 2 dark in ground colour with clear grey pollinosity, slightly darkened dorsally in the centre and with a very narrow pale yellowish margin; T3 and T4 with dark ground colour, only very narrowly pale yellowish along hind margins, both silvery-grey pollinose with large black median and sublateral spots, the latter extending indefinitely round the dorso-lateral surface; T5 with dark ground colour and silvery-grey pollinosity, with large bold black median and sublateral spots, the latter rounded and widely separated by grey pollinose areas from a smaller pair of blackish lateral spots; T7 + 8 with bold black median and sublateral spots, otherwise silvery-grey pollinose; epandrium black with yellowish-grey pollinosity. The median spots of each tergite parallel-sided and together more or less forming a long black median vitta, the grey pollinose areas greenish or bluish in some lights. Venter blackish with grey pollinosity, lobes of sternite 5 and paralobes of hypopygium shining reddish-brown. Tergites without specialised bristling, lateral marginal setae of T5 long and fine and widely spaced. Hypopygium (Fig. 64) with very large clavate paralobes each of which bears a long densely bristled process anteriorly. *Measurements*: body length 5.3 mm (range 5.2 to 5.4 mm), wing length 5.3 mm (5.2 to 5.4 mm) [3 specimens].

♀. Generally similar to ♂ with yellow legs, flattened hind metatarsus, and entirely hyaline wings. Differs from ♂ in having normal bristling to mid coxa, lacking the fine erect hair ventrally on mid and hind femora, and in having more distinct mesonotal vittae. Abdomen more or less entirely dark in ground colour with silvery-grey pollinosity (slightly greenish in some lights as in ♂), tergites 3–5 each with large bold slightly shining black median and sublateral spots, the latter extending round to the ventral surface on T3 and T4 but isolated by narrow grey pollinose areas from a pair of large black ventro-lateral spots on T5; T1 + 2 indistinctly blackish medially; tergites with indefinitely pale hind margins. T4 without median discal setae, T5 with a pair of long fine median discal setae. *Measurements*: body length 6.0, 6.2 mm, wing length 5.6, 5.7 mm [2 specimens].

Affinities

Very closely related to *P. cheesmanae* sp. n., as indicated by the very close resemblance of the ♂ genitalia (cf. Figs. 64 and 66), but easily distinguished in both

sexes by the brown antennae and in the ♂ by the dense fringe of bristles on the mid coxa.

Material examined

Holotype ♂, N.E. NEW GUINEA: Miramar, Asaro V., 1800 m, 27.vi.1955 (*J. L. Gressitt*). In the Bernice P. Bishop Museum, Honolulu. Paratypes: 1 ♂, N.E. NEW GUINEA: Nondugl, 2200–2700 m, 28.v.1959, (*C. D. Michener*) (Bishop Mus.); 1 ♂, N.E. NEW GUINEA: Nonguag, Asaro-Chimbu Div., 2500 m, 29.vi.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.); 1 ♀, N.E. NEW GUINEA: Daulo Pass area, 2500 m, 5.vii.1957 (*D. E. Hardy*) (Bishop Mus.); 1 ♀, N.E. NEW GUINEA: Mt. Otto, 2200 m, 22.vi.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♀, N.E. NEW GUINEA: Nondugl, 1600 m, 9.vii.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.).

In addition to the material listed above I have seen two females which may belong to this species but in which the apices of the mid and hind femora are dark brown and the fore femora brown dorsally near the apex; the data as follows: N.E. NEW GUINEA: Mt. Otto, 2200 m, 24.vi.1955 (*J. L. Gressitt*) (Bishop Mus.), and Miramar-Gobayabo, Asaro V., 2000 m, 29.vi.1955 (*J. L. Gressitt*) (B.M.Nat.Hist.).

Distribution

Known only from the above-listed material and probably confined to upland New Guinea.

***Pygophora dolabra* sp. n.**

Diagnosis

♂. Abdomen as in Fig. 67 with the postabdomen very distinctly set off from the preabdomen, T5 very large and almost as long as three preceding tergites together, T7 + 8 relatively small; ♂ hypopygium as in Fig. 68 and sternite 5 very complex (Fig. 123); ♂ *pv* seta of fore tibia exceptionally long (for this sex), longer than distance from its insertion to apex of tibia.

Description

♂. *Head*: occiput grey pollinose over blackish ground colour, latter contrasting with yellow ground colour of the genae. Frons very narrow. Interfrontal area deep yellow or orange-yellow, slightly brownish-yellow posteriorly. Face and parafacials densely yellow pollinose, parafrontals deep golden-yellow pollinose. Ocellar setae fine, about equal in length to or somewhat shorter than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange-yellow, third segment about 2.4 times as long as second segment and falling short of mouth-margin by about three-quarters of its length; arista long-plumose on basal third. Palpi yellowish-white. Mentum yellow or slightly brownish-yellow. *Thorax*: ground colour black, humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely grey pollinose, dorsum yellowish-grey pollinose (mesonotal pollinosity between the dorsocentral rows distinctly yellow in some lights) with traces of narrow blackish *dc* vittae. Acrostichal hairs in a single median row, sometimes in a slightly irregular close-set double row presuturally; no *dc* setula preceding the *prst dc* seta; two *post*

ia setae present. *Wings*: rather elongate with cross-vein *r-m* unusually far beyond apex of vein R_1 , basally hyaline but pale smoky greyish-brown on apical third with the infuscation most intense anteriorly and on the veins. Calyptrae white with white fringes. Halteres yellow. *Legs*: mostly yellow but fore tarsi brown from apical third of metatarsi to the apices, other tarsi slightly brownish distally, mid and hind coxae mostly reddish-brown with pale grey pollinosity. Fore tibia with two *ad* setae, the *pv* seta exceedingly long (for ♂ sex) and appreciably longer than distance from its insertion to tibial apex, the *pv* seta not standing out from the tibia as erectly as usual. Mid coxa weakly bristled; mid femur with two preapical *p* setae, without specialised bristling, the *pv* setae very fine; mid tibia without an *ad* seta, the two *pd* setae about three and four times as long as tibial diameter. Hind femur with the usual two very long fine submedian *pv* setae in addition to some smaller *pv* setae; hind tibia without a preapical lobe or *pv* setae, the setae of extensor surface fine and the distal *ad* seta very long, the *d* preapical seta slightly shorter than hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 67): of characteristic form with the postabdomen very distinctly set off from the preabdomen, T7 + 8 very small in comparison with T5 which is very large and almost as long as three preceding segments together, sternite 5 very complex with movable lateral lobes (after potash treatment and mounting as in Fig. 123). T1 + 2, T3 and T4 pale reddish-yellow with thin white pollinosity, T1 + 2 either entirely without darker colouring or with a small indistinct median brownish area, T3 with a narrow median red-brown line which is sometimes expanded laterally but without sublateral spots, T4 with bold black-brown median and sublateral spots separated by pale grey or whitish pollinose areas, the sublateral spots triangular and extending a little way on to the dorso-lateral surfaces of the tergite; T5 blackish in ground colour (except for a broad pale reddish-yellow ventral margin) with pale grey or yellowish-grey pollinosity and large black median and sublateral spots, the latter rounded or subquadrate in shape and the median spot subtriangular and not reaching anterior margin of the tergite (median abdominal spots therefore not forming a median vitta); T7 + 8 and epandrium blackish with pale grey pollinosity, T7 + 8 with a bold black median dorsal lunate spot but without sublateral spots. Venter yellowish, median part of sternite 5 blackish, lobes of sternite 5 and paralobes of hypopygium shining reddish-yellow. Tergites without specialised bristling, ventro-lateral margin of T5 with five or six long fine subequal setae. Hypopygium (Fig. 68) with very large clavate paralobes and complex mesolobe, each paralobe on inner surface with several stout black spines. *Measurements*: body length 6.6 mm (range 6.5 to 6.6 mm), wing length 6.1 mm (range 6.0 to 6.2 mm) [5 specimens].

♀. Generally like the ♂ with legs of the same colouring and wings darkened apically, but basal two-thirds of wings slightly yellowish tinged (not clear hyaline) and apical dark area more distinctly brown. Abdomen with T1 + 2 largely yellowish but with a large dark reddish-brown median area and indefinitely darkened anteriorly; T3 and T4 both mainly dark in ground colour and only pale reddish-yellow along posterior margins and to some extent ventro-laterally on T3, each with large brownish-black median and sublateral spots separated by grey pollinose areas, the median spots parallel-sided and extending the length of the tergite,

the sublateral spots more or less extending round laterally to the ventral surface; T5 dark with grey pollinosity and a pair of large rounded black sublateral spots and a less distinct broad median blackish line, ventro-laterally with a pair of blackish spots narrowly separated from the sublateral spots. T4 without median discal setae, T5 with a strong pair of median discal setae. Measurements: body length 6.85 mm (range 6.5 to 7.4 mm), wing length 6.5 mm (range 5.9 to 6.8 mm) [6 specimens].

Affinities

P. dolabra is a distinctive species easily recognisable in the ♂ by the form of the abdomen and genitalic structure, and its general affinities appear to be with *P. cheesmanae* sp. n. and *P. villicoxa* sp. n. in which there are somewhat similar clavate paralobes to the hypopygium (though this resemblance may be convergent and may not indicate close affinity).

Material examined

Holotype ♂, NEW GUINEA: Papua, Minj, W. Highlands, 8-13.ix.1959 (*T. C. Maa*). In the Bernice P. Bishop Museum, Honolulu. Paratypes: 3 ♂♂, data as for holotype (Bishop Mus. and B.M.Nat.Hist.); 1 ♂, N.E. NEW GUINEA: Sinofi, 30 km. S. of Kainantu, 1590 m, 4.x.1959 (*T. C. Maa*) (Bishop Mus.); 1 ♂, N.E. NEW GUINEA: Mt. Otto, 2200 m, 23.vi.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♂, DUTCH NEW GUINEA: Waris, S. of Hollandia, 450-500 m, 8-15.viii.1959 (*T. C. Maa*) (B.M.Nat.Hist.); 1 ♀, N.E. NEW GUINEA: Lae, sea-level, 23.vii.1955 (*J. L. Gressitt*) (Bishop Mus.); 1 ♀, N.E. NEW GUINEA: W. Highlands, Baiyer R., 1150 m, 18.x.1958 (*J. L. Gressitt*) (B.M.Nat.Hist.); 2 ♀♀, N.E. NEW GUINEA: Kassam, 48 km. E. of Kainantu, 7.ix.1959 and 28.x.1959 (*T. C. Maa*) (Bishop Mus.); 1 ♀, DUTCH NEW GUINEA: Bodem, 11 km. S.E. of Oerberfaren, 100 m, 7-17.vii.1959 (*T. C. Maa*) (Bishop Mus.); 1 ♀, DUTCH NEW GUINEA: Ifar, 300-600 m, 20.vi.1959 (*T. C. Maa*) (B.M.Nat.Hist.).

Distribution

Evidently an endemic species confined to New Guinea, where it appears to be widely dispersed from sea-level at least to 2200 metres (7150 ft.).

***Pygophora brandti* sp. n.**

Diagnosis

Large species, ♂ easily distinguished by form of the lobes of sternite 5 (Fig. 69) and the hypopygium (Fig. 70).

Description

♂. *Head*: occiput pale grey pollinose except near the eye-margins where it is slightly yellowish. Interfrontal area deep orange-yellow or slightly brownish-yellow, the colour darkening slightly posteriorly to reddish-orange or reddish. Face whitish-yellow pollinose, parafacials pale yellow pollinose, parafrontals darker golden yellow pollinose. Ocellar setae very long and fine, much longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper

and lower pairs of inclinate frontal setae. Antennae yellow-orange, slightly brownish-yellow on second segment, third segment about 2.4 times as long as second segment and falling short of mouth-margin by about three-quarters of its length; arista long-plumose on basal third. Palpi yellowish-white. Mentum yellow-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pollinosity of thorax dark grey but very slightly yellowish on the mesonotum between the narrow blackish *dc* vittae, slight trace of a darker grey median vitta present, areas outside *dc* vittae dark slightly bluish-grey in certain lights. Acrostichal hairs in a single median row, sometimes a little irregular, except for pair of fine prescutellar hairs; *prst dc* seta not preceded by a *dc* setula; two fine *post ia* setae present (one side of holotype possesses only one). *Wings*: very slightly smoky basally and with a more definite smoky brownish suffusion apically, the brown colour more definite and darker preapically on the anterior margin. Calyptrae whitish with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for most of the mid coxa which is blackish with grey pollinosity. Fore tibia with two small *ad* setae, the *pv* seta fine and about three-quarters as long as distance from its insertion to apex of tibia, the *d* preapical seta rather long and fine. Mid femur with two preapical *p* setae, without specialised bristling; mid tibia without an *ad* seta, the two *pd* setae long and about four and five times as long as tibial diameter. Hind femur without specialised bristling, with the usual three long fine *pv* setae; hind tibia without a preapical lobe or *pv* setae, the setae of the extensor surface very long and sometimes slightly sinuous, the *d* preapical seta about equal in length to hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 69): long and rather narrow but not at all laterally flattened towards the apex, most of the ventral surface formed by the very enlarged sternite 5 with its long acuminate lateral lobes, T7 + 8 long and bearing the epandrium in a terminal position. T1 + 2 mainly yellowish but with a large brown mark dorsally; T3 and T4 each extensively yellow laterally and narrowly along the hind margins elsewhere, each with a bold brownish-black median and sublateral pair of spots separated by silvery-grey pollinose areas, the sublateral spots extending laterally around the sides of the tergites (especially on T4); T5 mainly blackish in ground colour except for an indistinct paler margin ventrally, silver-grey pollinose with a bold black median spot and a pair of bold black sublateral spots (the latter rounded in shape), the tergite also with an indistinct pair of very small blackish spots on either side below the sublateral spots; T7 + 8 black in ground colour and densely silver-grey pollinose with distinct rounded black median and sublateral spots; epandrium reddish-black with yellowish-grey pollinosity. Basal sternites mainly yellow, sternite 5 blackish with thin grey pollinosity basally and with shining red-brown lobes, paralobes of hypopygium also shining red-brown. Tergites without specialised bristling, the lateral marginal setae of T5 few and widely-spaced but long and fine. Hypopygium with very long narrow mesolobes and long more or less parallel-sided paralobes, the latter with numerous long fine curled hairs on their outer surfaces and hind margins (Fig. 70). *Measurements*: body length 7.7 mm (range 7.6 to 7.8 mm), wing length 7.0 mm (range 6.9 to 7.1 mm) [3 specimens].

♀. Generally very similar to ♂ with blackish *dc* vittae (especially evident to

naked eye) and similar smoky apices to the wings; the wings are more yellowish basally in the single ♀ seen. Abdomen with T1 + 2 yellowish laterally but mainly blackish-brown dorsally; T3 and T4 both mainly dark in ground colour but narrowly pale yellowish on apical margins, each with large shining very dark brownish-black median and sublateral spots, the sublateral "spots" very large and extending round to the ventral side so that they occupy almost all the dorso-lateral aspects of the tergites, areas between median spot and sublateral spots densely grey pollinose; T5 dark with dense silvery-grey pollinosity and large black median and sublateral spots. T4 without median discal setae and with rather weak marginals, T5 with a pair of very strong median discal setae standing on each side of the boldly marked median spot. Measurements: body length 7.1 mm, wing length 6.9 mm [1 specimen].

Affinities

An unusually large species easily recognised in the ♂ by the structure of the postabdomen; although the hypopygium is very different the general affinities appear to be with *P. dolabra* sp. n., also from New Guinea.

Material examined

Holotype ♂, N.E. NEW GUINEA: Eliptamin Valley, 1200–1350 m, 16–31.vii.1959 (W. W. Brandt). In the Bernice P. Bishop Museum, Honolulu. Paratypes: 3 ♂♂, same locality and collector as holotype, 1–15.viii.1959 and 16–30.viii.1959 (Bishop Mus. and B.M.Nat.Hist.); 1 ♀, same locality and collector as holotype, 1–15.ix.1959 (Bishop Mus.).

Distribution

Known only from the type locality of Eliptamin Valley in north-eastern New Guinea.

Pygophora seticornis sp. n.

Diagnosis

♂. Distinguished from all other known species by the presence of several small bristles antero-internally on the third antennal segment near the insertion of the arista (Fig. 32).

Description

♂. *Head*: occiput grey pollinose, becoming pale yellowish pollinose near the eye-margins. Interfrontal area deep orange anteriorly and darkening to reddish-orange posteriorly. Face and parafacials pale yellow pollinose, but orange ground colour of parafacials distinct; parafrontals blackish in ground colour (contrasting with the parafacials) with thin golden pollinosity. Ocellar setae long and fine, longer than upper reclinate frontal setae. Parafrontals with strong supernumerary inclinate setae between upper and lower pairs of inclinate frontal setae, in the holotype two such supernumeraries on one side and three on the other, and with one or two very small hairs in addition to the supernumerary setae. Antennae brownish-orange on basal two segments, third segment bright orange on basal quarter and brown on apical three-quarters, the third segment with a few (in the holotype three on

one antenna and five on the other) bristly hairs on the inner surface anteriorly near the base of the arista (Fig. 32), the third segment about 2.5 times as long as second segment and falling short of mouth-margin by about four-fifths of its length; arista plumose only on basal third. Palpi yellowish-white. Mentum shining dark brown. *Thorax*: blackish in ground colour, humeral calli and scutellum concolorous with rest of mesonotum; dorsum densely brownish-yellow pollinose except for two pale grey pollinose areas on the anterior margin of the prescutum on either side of the first pair of presutural acrostichal setae; mesonotum without vittae and with a very slight greenish tinge laterally in certain lights; pleurae badly greased in holotype but probably densely greyish-yellow pollinose; metanotum pale grey pollinose and contrasting with yellowish scutellum and mesonotum. Prescutum with two very strong pairs of *prst acr* setae, the postsutural acrostichals much weaker; 2 + 3 *dc* setae present, the pair of very small *dc* setulae in front of the *prst dc* setae of other species being greatly developed as a definite pair of strong dorsocentrals; two very strong *post ia* setae present. *Wings*: with a faint yellowish-brown tinge in the anterior half but without definite dark preapical spot. Upper calypter slightly smoky brownish with pale yellowish-brown fringe-hairs, lower calypter yellowish with yellowish-white fringe. Halteres yellow. *Legs*: mainly reddish-yellow including fore coxae, but dorsal surface of fore femora and apical half or two-thirds of dorsal surfaces of mid and hind femora blackish-brown or dark reddish-brown. Fore tibia with two very strong *ad* setae and with one or two smaller *ad* setulae distinguishable from the tibial hairs, the *pv* seta a little shorter than the distance from its insertion to apex of tibia. Mid coxa with weak ventro-apical setae; mid femur with two preapical *p* setae, without specialised bristling, *pv* surface with four long setae and several smaller setae between and beyond these; mid tibia without an *ad* seta, the two *pd* setae about two and three and a half times as long as tibial diameter. Hind femur with two very long *pv* setae near the middle; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about equal in length to hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 71): broad and deep with very enlarged sternite 5. Abdomen of holotype badly greased but probably mainly blackish in ground colour with dense yellowish-grey pollinosity, in parts with a greenish tinge, and probably with a pattern of blackish median and sublateral spots on each tergite; lateral lobes of sternite 5 and paralobes of hypopygium shining yellowish-red. Tergites without specialised bristling, lateral marginal setae of T5 very long and fine but not very close-set and subequal in length. Hypopygium with short and rather broad paralobes which are slightly curved forwards and acuminate apically, each paralobe bearing long fine hairs on the outer surface. *Measurements*: body length 6.3 mm, wing length 6.2 mm [1 specimen].

♀. Unknown.

Affinities

P. seticornis is easily distinguished (♂) from all other species at present known by the bristles on the third antennal segment and by the two pairs of very strong *prst acr* setae, but the shape of the head, bristling of the parafrontals, the shape of sternite 5 and other characters indicate general affinity with *P. villicoxa* sp. n.

and to a lesser extent with *P. cheesmanae* sp. n. (both of which are also from New Guinea).

Material examined

Holotype ♂, N.E. NEW GUINEA: Miramar-Gobayabo, Asaro, 2000 m, 29.vi.1955 (*J. L. Gressitt*). In the Bernice P. Bishop Museum, Honolulu. No other material known.

Distribution

Known only from the type locality in north-eastern New Guinea.

Pygophora nitidiventris Malloch, 1929

Pygophora nitidiventris Malloch, 1929, *Treubia* 7: 396. Holotype ♀, BURU. In the Zoölogisch Museum, Amsterdam.

Diagnosis

♀. With a pair of very small supernumerary inclinate setae on the parafrontals between the upper and lower pairs of inclinate frontal setae, frons broad, fore tibia without *ad* setae, abdomen yellow with each tergite having a very broad shining dark red-brown transverse fascia which occupies most of the dorsum of the tergite.

Description

♀. *Head*: occiput thinly greyish-white pollinose over a dark brownish ground colour. Frons broad. Interfrontal area bright orange-yellow but with some white pollinosity so that in certain lights it appears yellowish-white. Face whitish pollinose, parafacials and parafrontals very pale yellowish-white pollinose. Ocellar setae very strong and much longer than upper reclinate frontal setae. Parafrontals with a pair of very small fine supernumerary inclinate setae between the upper and lower pairs of inclinate frontal setae, each parafrontal also with one or two minute hairs just below the lowest (strongest) inclinate frontal seta. Antennae pale orange-yellow, third segment about 3 times as long as second segment and falling short of mouth-margin by about a quarter of its length; arista very long-plumose on basal three-fifths. Palpi pale yellow. Mentum light yellow-brown. *Thorax*: ground colour entirely blackish-brown or very dark reddish-brown, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and dorsum rather thinly grey pollinose, the thorax appearing slightly shining brown when viewed from behind but grey when seen from in front; mesonotum with a faint yellowish-brown pollinose median *acr* vitta and in certain lights with very narrow traces of blackish *dc* vittae. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a very small *dc* setula; two well developed *post ia* setae present. *Wings*: yellowish hyaline. Calyptrae white or yellowish-white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for the extreme bases of the mid coxae which are reddish-brown with grey pollinosity. Fore tibia without *ad* setae. Mid femur with two preapical *p* setae and with the usual (♀) three long *pv* setae in the basal half; mid tibia without an *ad* seta. Hind femur with two or

three long *pv* setae in basal half; hind tibia without *pv* setae. *Abdomen*: basic colour yellow, but each tergite with a very broad dark red-brown transverse shining fascia which fills most of the dorsal surface of the tergite so that the yellow colour is mainly visible only at the fore and hind margins and on the sides of T1 + 2; abdomen therefore without spots and almost completely without the usual grey pollinosity, although very slight traces of pale greyish pollinosity are visible antero-laterally on each tergite (just behind the preceding tergite) in certain lights. Abdominal setae very strong, especially the marginal setae of T4, T4 without median discal setae, T5 with a pair of very strong erect median discal setae in additon to the strong lateral discal setae. *Measurements*: body length 3.75, 4.2 mm, wing length 3.5, 3.9 mm [2 specimens].

♂. Unknown.

Affinities

Although the ♂ is not yet known it is evident, from the size, abdominal pattern, the absence of *ad* setae on the fore tibiae, and the presence of a small pair of supernumerary inclinate frontal setae, that *P. nitidiventris* is closely allied to *P. argentea* Paramonov; the ♀ differs however from the ♀ *argentea* by having a broader frons, an all orange-yellow interfrontal area (instead of the largely dark reddish or purplish-brown colour of *argentea*), and much weaker supernumerary setae on the parafrontals.

Material examined

Holotype ♀, BURU (Indonesia): Station 9, 19.v.1921 (*L. J. Toxopeus*). SUMATRA: 1 ♀, Fort de Kock, 920 m, 1925 (*E. Jacobson*) (U.S.Nat.Mus.). MALAYA: 1 ♀, Selangor, Bukit Kutu, 3500 ft, 20.iv.1926 (*H. M. Pendlebury*) (B.M.Nat.Hist.).

Distribution

Only known from the localities listed above.

Pygophora argentea Paramonov, 1961

Pygophora argentea Paramonov, 1961, *Ann. Mag. nat. Hist.* (13) 3: 506. Holotype ♂, QUEENSLAND. In the Division of Entomology Museum, C.S.I.R.O., Canberra.

Diagnosis

Very small species without *ad* setae on fore tibiae, arista plumose almost to the tip, parafrontals with a supernumerary pair of inclinate setae, abdomen without spots but last two or three tergites each with a broad nearly black or dark brown transverse fascia almost filling the dorsum of the tergite, thorax densely silver or silvery-grey pollinose viewed from in front but dark blackish-brown viewed from behind (shifting appearance more evident in ♂); ♂ interfrontal area bright silver pollinose as the parafrontals so that from most angles the entire frons appears bright silver, lateral lobe of sternite 5 as in Fig. 116.

Description

♂. *Head*: occiput silvery-grey pollinose. Interfrontal area entirely covered with

dense silvery pollinosity like that on the parafrontals so that the entire frons appears bright silver in most lights, in certain lights ground colour of interfrontal area seems to be orange anteriorly and dark brown posteriorly. Face and parafacials silvery-white pollinose, parafrontals silvery pollinose as the interfrontal area. Ocellar setae unusually long but fine, almost as long as *lower* reclinate frontal setae. Parafrontals with a supernumerary pair of small fine inclinate setae between the upper and lower pairs of inclinate frontal setae. Antennae mainly yellow, slightly brownish-yellow on second segments and third segments darkening to brownish on apices, third segment about 3.5 times as long as second segment and falling short of mouth-margin by about a quarter of its length; arista plumose on basal three-quarters, only the tip bare, the plumosity shorter than usual. Palpi yellowish-white. Mentum dark yellowish-brown. *Thorax*: ground colour entirely dark blackish-brown, humeral calli and scutellum concolorous with rest of mesonotum, appearance of the dorsum of the thorax changing with the angle of the light with the mesonotum brilliantly and densely silvery pollinose viewed from in front but semi-shining blackish-brown viewed from behind; traces of dark *dc* vittae visible as the appearance changes when the fly is rotated; pleurae silvery-grey pollinose, with a similar but less distinct change to the dark ground colour when viewed from behind. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a small *dc* setula; two *post ia* setae present. *Wings*: with a very faint smoky yellowish tinge especially in the apical half. Calyptrae pale yellowish-white with white fringes. Halteres pale yellow. *Legs*: entirely yellow, including the coxae. Fore tibia without *ad* setae, the *pv* seta small and only half as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, without specialised bristling, the setae of the *av* and *pv* rows rather short and fine; mid tibia without an *ad* seta, the two *pd* setae short but rather strong and about as long as tibial diameter. Hind femur with two long fine *pv* setae in basal half; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta unusually short and little more than a third as long as the hind metatarsus; hind tarsus simple. Claws of all legs unusually small. *Abdomen* (Fig. 34): not strongly laterally compressed, T5 not forming a dorsal keel, but in dorsal view noticeably contracted towards the apex, lateral lobes of sternite 5 long and narrow and acuminate at the apices (Fig. 116). T1 + 2 and most of T3 yellowish, T3 dorsally with a narrow yellowish-brown transverse fascia which is developed medially into a triangular mark; T4 and T5 dorsally both almost completely semi-shining dark brownish-black without spots and with only narrow traces of greyish pollinosity antero-laterally, both tergites pale reddish-yellow ventro-laterally; T7 + 8 dorsally and dorso-laterally semi-shining brownish-black except for a broad transverse anterior densely grey pollinose band, brownish-orange apically; epandrium yellowish-orange with inconspicuous thin whitish pollinosity. Venter partly blackish, lobes of sternite 5 bright yellow-orange and pollinose (not translucent), paralobes of hypopygium yellowish-orange. Tergites without specialised bristling but the discal and marginal setae very strong, T4 with a pair of strong erect median marginal setae. *Measurements*: body length 3.7 mm, wing length 3.2 mm [1 specimen].

♀. Generally like the ♂ with only the tips of the aristae bare and lacking *ad* setae on fore tibiae. Interfrontal area reddish or bright orange near the lunula and becom-

ing reddish or purplish-brown posteriorly, not conspicuously silver pollinose and therefore obviously contrasting with the parafrontals. Thorax grey pollinose with traces of brownish-grey pollinose vittae, less silvery than ♂ and with the shifting appearance less pronounced, although the mesonotum is obviously brown when viewed from behind. Abdomen slightly shining, T1 + 2 and T3 reddish-yellow each with a median longitudinal reddish-brown line; T4 partly reddish-yellow but with a broad dark brown transverse fascia occupying most of the dorsal surface; T5 with a similar broad dark reddish-brown transverse fascia filling most of the dorsum but reddish-orange apically and with yellowish pollinosity antero-laterally. T4 without median discal setae but the marginal setae very strong, T5 with a very strong pair of median discal setae in addition to the lateral discal setae. Measurements: body length 4.2, 4.4 mm, wing length 3.9, 4.0 mm [2 specimens].

Affinities

P. argentea is closely allied to *P. nitidiventris* Malloch (the ♂ of *nitidiventris* is not known and *argentea* could be synonymous with *nitidiventris*, but this is not very likely). Both *argentea* and *nitidiventris* possess supernumerary inclinate setae, lack *ad* setae on fore tibia, have the arista plumose on most of its length and similar broad semi-shining transverse dark fasciae on the posterior tergites of the abdomen. In some respects *P. argentea* shows affinities also with *P. longipila* (Stein) and *P. enigma* sp. n. which also lack *ad* setae on the fore tibia, but these species possess definite abdominal spots.

Material examined

Holotype ♂, AUSTRALIA: Queensland, 4 mls. S. of Atherton, 2.vi.1955 (*K. R. Norris*). AUSTRALIA: 1 ♀, Queensland, Mt. Bartle Frere, East Base, 80 ft., 24.iv.1955 (*Norris* and *Common*) (Div.Ent.Mus.Canberra); 2 ♀♀, Queensland, — (—) (B.M.Nat.Hist.).

Distribution

Only known from Queensland, Australia, and possibly confined to this territory.

***Pygophora flavida* sp. n.**

Diagnosis

Distinguished in both sexes from all other known species of *Pygophora* by the pale reddish-yellow colour of the thorax; arista plumose almost to the tip, parafrontals with at least a minute pair of supernumerary setae between upper and lower pairs of inclinate frontal setae, fore tibia without *ad* setae; ♂ hypopygium with minute paralobes (Fig. 107), sternite 5 as in Fig. 119.

Description

♂. *Head*: occiput thinly white pollinose over yellowish or pale brownish ground colour. Interfrontal area yellow. Face, parafacials and parafrontals pale yellow pollinose. Ocellar setae well developed, longer than upper reclinate frontal setae. Parafrontals with a pair of well developed setae or at least a pair of minute setulae between the upper and lower pairs of inclinate frontal setae. Antennae pale yellow,

third segment about 3.8 to 4 times as long as second segment and falling short of mouth-margin by about one-sixth of its length; arista long-plumose for most of its length, only extreme tip bare. Palpi yellowish-white. Mentum yellow. *Thorax*: almost completely pale reddish-yellow, with only some limited brown colouring on the mesonotum and a little thin white pollinosity; mesonotum with a brown median *acr* vitta which is broadened into a larger brown or reddish-brown prescutellar area between the two hindmost pairs of *post dc* setae, and with less distinct reddish-brown *dc* vittae which also more or less unite posteriorly with the darkened prescutellar area. Presutural acrostichal hairs in two rows; no *dc* setula preceding the *prst dc* seta; two *post ia* setae present. *Wings*: short and broad with a pale yellowish tinge. Calyptrae pale yellowish, upper calypter with slightly darkened margin, fringe hairs pale yellow. Halteres yellow. *Legs*: entirely yellow or pale reddish-yellow, including all the coxae. Fore tibia without *ad* setae, the *pv* seta very short and less than half as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, without specialised bristling; mid tibia without an *ad* seta, the two *pd* setae very short and strong and only about as long as tibial diameter. Hind femur with a very long submedian *pv* seta and a shorter seta nearer the base; hind tibia without a preapical lobe or *pv* setae, setae of extensor surface short and strong, the *d* preapical seta extremely short and only about one-quarter or one-fifth as long as hind metatarsus; hind tarsus simple. *Abdomen*: short and deep, slightly laterally compressed but T5 not at all produced into a flattened dorsal keel, epandrium very large, lateral lobes of sternite 5 shaped as in Fig. 119 and bearing long fine hairs. Abdominal colour mainly reddish-yellow, somewhat pale translucent yellowish basally, with very thin white pollinosity; T4, T5 and T7 + 8 indistinctly darker semi-shining reddish or brownish dorsally, T4 (? T5 normally as well) with a pair of large brown areas which nearly meet in the mid-line (possibly sometimes coalescing to form a broad transverse brown fascia across the tergite). Venter yellow, lobes of sternite 5 and paralobes of hypopygium reddish-yellow, epandrium reddish-orange. Tergites without specialised bristling, the ventro-apical marginal setae very small and inconspicuous. Hypopygium (Fig. 107) with extremely small paralobes and large aedeagus. *Measurements*: body length 4.4, 4.1 mm, wing length 3.7, 3.4 mm [2 specimens].

♀. Closely similar to ♂. Abdomen mainly reddish-yellow, T3, T4 and T5 each with a pair of very large dark brown or yellowish-brown marks, those on T5 clearly separated by yellow ground colour but those on T3 and T4 sometimes more or less coalesced in the mid-line so that these two tergites show broad brown fasciae transversely across the segments, spots on T3 sometimes evanescent. T4 without median discal setae, T5 with a pair of strong median discal setae. *Measurements*: body length 4.9 mm (range 4.5 to 5.2 mm), wing length 4.4 mm (range 4.1 to 4.7 mm [6 specimens]).

Affinities

P. flavida is a distinctive species easily distinguished by the general reddish-yellow colouring (not otherwise found in *Pygophora* although common in *Cephalispa* Malloch); its affinities, as shown by the lack of *ad* setae on the fore tibiae, the plumosity of the arista, the presence of supernumerary parafrontal setae, nature

of the abdominal marking and the shortness of the leg setae are with *P. argentea* Paramonov and *P. nitidiventris* Malloch, and perhaps to a lesser extent with *P. longipila* (Stein).

Material examined

Holotype ♂, DUTCH NEW GUINEA: Hollandia area, W. Sentani, Cyclops Mts., 200–1000 m., 16–18.vi.1959 (*T. C. Maa*). In the Bernice P. Bishop Museum, Honolulu. Paratypes: 4 ♂♂, 9 ♀♀, same locality and collector as holotype, 16–25.vi.1959 (Bishop Mus. and B.M.Nat.Hist.).

In addition two females have been seen which differ slightly from the type series, but which are probably assignable to *P. flavida*. These specimens are a little larger and the mesonotum is more or less all dark brown between the rows of *dc* setae. The data are: NEW GUINEA: Papua, Minj, W. Highlands, 8–13.ix.1959 (*T. C. Maa*) (Bishop Mus.) and N.E. NEW GUINEA: Kumur, Upper Jimmi V., 100 m., 13.vii.1955 (*J. L. Gressitt*) (Bishop Mus.).

Distribution

Probably an endemic species confined to New Guinea and known only from the material listed above.

Pygophora longipila (Stein, 1910) **comb. n.**

Coenosia longipila Stein, 1910, *Ann. hist.-nat. Mus. hung.* **8**: 565. Lectotype ♂, NEW GUINEA. In the Zoologisches Museum der Humboldt-Universität, Berlin.

Lectotype designation: Stein described *C. longipila* from three ♂ and two ♀ syntypes, most of which were in the Budapest Museum and were destroyed in 1956. Only one ♂ syntype now exists (in Zool.Mus.Humb.Univ.) and this has been selected and labelled as lectotype.

Diagnosis

Very small species, ♂ with frons broader than usual, fore tibia without *ad* setae, arista plumose along most of its length (Fig. 29), hypopygium as in Fig. 78.

Description

♂. *Head*: occiput pale grey pollinose. Frons unusually broad for the genus. Interfrontal area deep yellow. Face, parafacials and parafrontals white pollinose, the parafrontals therefore strongly contrasting in colour with the yellow interfrontal area. Ocellar setae well developed, longer and stronger than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellow-orange, third segment about 2.8 times as long as second segment and falling short of mouth-margin by about a quarter of its length; arista sparsely long-plumose on the basal four-fifths, only the tip bare (Fig. 29). Palpi pale yellow. Mentum yellow-brown. *Thorax*: ground colour entirely dark reddish-brown to blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae and dorsum densely grey pollinose, the mesonotum slightly bluish-grey in certain lights and without vittae. Presutural acrostichal

hairs in two rows, one pair developed as strong *acr* setae; a small but distinct *dc* setula differentiated in front of the *prst dc* seta; only one well developed *post ia* seta which is preceded by two smaller *ia* setulae, the median one of the three of intermediate size. *Wings*: with an exceedingly faint yellowish tinge. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow including the coxae. Fore tibia without *ad* setae, the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, without specialised bristling; mid tibia without an *ad* seta, the two *pd* setae two and three times as long as tibial diameter. Hind femur with a very strong and long *pv* seta at about one-third from the base and a much smaller finer and less conspicuous *pv* seta on either side of this; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta only a little more than half as long as hind metatarsus; hind tarsus simple. *Abdomen*: subcylindrical in form, not noticeably laterally compressed, lateral lobes of sternite 5 large. T1 + 2 and most of T3 yellow, T3 with a median dark reddish-brown mark; T4 with blackish-brown median and sublateral spots separated by grey pollinose areas, pale reddish-yellow ventro-laterally; T5 with large blackish-brown median and sublateral spots separated by grey pollinose areas and reddish-yellow ventro-laterally, generally similar to T4; T7 + 8 entirely reddish with grey pollinosity; epandrium reddish-orange. Venter, lobes of sternite 5, and paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, the dorsal marginal setae of T4 and T5 very strong, but the ventro-apical marginal setae of T5 very short and weak. Hypopygium as in Fig. 78, paralobes with a curious black socketed process on the hind margin. *Measurements*: body length 3.4 mm, wing length 3.0 mm [1 specimen].

♀. No material seen, but according to Stein (original description) generally like the ♂ but abdomen not at all translucent yellowish at the base and entirely grey coloured (presumably with dark spots on T4 and T5 and probably T3). Length given by Stein as 4 mm.

Affinities

P. longipila appears to be a rather isolated (allied closely only to *P. enigma* sp. n.) species in which the paralobes of the ♂ hypopygium are unlike those in other species; the lack of *ad* setae on the fore tibiae and the arista plumose on most of its length suggest, however, possible affinity with *P. argentea* Paramonov and *P. nitidiventris* Malloch.

Material examined

Lectotype ♂, NEW GUINEA: Huon Gulf, Simbang, 1899 (*Biro*).

Distribution

Known only from the type locality in eastern New Guinea.

***Pygophora enigma* sp. n.**

Diagnosis

♂. Hypopygium as in Fig. 93, frons unusually broad and arista plumose for three-quarters of its length, fore tibia without *ad* setae, antennae dark

brown and almost reaching mouth-margin, parafacials not fully visible in lateral view.

Description

♂. *Head*: occiput grey pollinose. Frons unusually broad for this genus as in *P. longipila* (Stein). Interfrontal area brownish-orange or dark brown. Face thinly greyish-white pollinose over brownish ground colour, parafacials dirty whitish pollinose with a yellowish ground colour evident dorsally and brownish ground colour more ventrally, parafrontals greyish-white pollinose. Ocellar setae well developed, longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae dark brown, only slightly orange dorsally on second segment and on extreme base of third segment, third segment long and about 3.8 times as long as second segment, almost reaching mouth-margin (falling short by only about one-eighth of its length); arista plumose on basal three-quarters, the hairs a little shorter than in most species. Palpi pale yellow. Mentum red-brown. *Thorax*: ground colour dark reddish-brown to blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale grey pollinose, mesonotum grey pollinose at the edges and anteriorly but otherwise largely brownish pollinose, disc of scutellum brownish pollinose. Presutural acrostichal hairs in two rows, one pair well developed as *acr* setae; no clearly differentiated *dc* setula present in front of the *prst dc* seta; only one *post ia* seta developed. *Wings*: with a very faint smoky brownish suffusion distally. Calyptrae yellowish-white with pale yellowish fringes, upper calyptra with slightly darkened margin. Halteres pale yellow. *Legs*: entirely yellow except for very slight darkening on mid coxae. Fore tibia without *ad* setae, the *pv* seta very fine and short, and less than half as long as distance from its insertion to apex of tibia. Mid femur with two preapical *p* setae, without specialised bristling; mid tibia without an *ad* seta, the two *pd* setae about two and three times as long as tibial diameter. Hind femur with a very long fine submedian *pv* seta and two outstandingly long *av* setae in apical third; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta half as long as hind metatarsus; hind tarsus simple. *Abdomen*: not laterally compressed, lateral lobes of sternite 5 large and shaped much as in *P. longipila* (Fig. 78). T1 + 2 and T3 yellowish, each with a median indefinite reddish-brown area; T4 and T5 both dark in ground colour, grey pollinose with blackish-brown median and sublateral spots, only narrowly reddish-yellow ventrally; T7 + 8 dark brownish with grey pollinosity and a median dorsal brown pollinose area; epandrium reddish-orange. Venter largely yellowish, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, the dorsal marginal setae of T4 and T5 very long and strong but set well forward on the tergites in a more or less discal position, ventro-lateral marginal setae short and weak. Hypopygium very like that of *longipila* (cf. Figs. 93 and 78), paralobes differing slightly in shape. *Measurements*: body length 4.1 mm, wing length 3.8 mm [1 specimen].

♀. Unknown.

Affinities

P. enigma is a puzzling species which is almost identical in some respects with,

and certainly very closely allied to, *P. longipila* (Stein). The ♂ genitalia of the two forms differ only very slightly and the difference could possibly be attributable to variation within the one species (*longipila*); however the antennae in this new form are much longer than in *longipila* and nearly reach the mouth-margin, and furthermore are dark brown instead of yellow, the arista has shorter plumose hairs, the interfrontal area is brownish-orange or dark brown, and there are several other minor differences. Both forms have the rather broad frons. On balance the differences from *P. longipila* (lectotype only of which is known to me) justify the description of *P. enigma* as a new species.

Material examined

Holotype ♂, N.E. NEW GUINEA: Mt. Otto, 2200 m., 23.vi.1955 (*J. L. Gressitt*). In the Bernice P. Bishop Museum, Honolulu. Paratype ♂, N.E. NEW GUINEA: Kassam, 48 km E. of Kainantu, 1350 m., 7.xi.1959 (*T. C. Maa*) (B.M.Nat.Hist.).

Distribution

Known only from north-eastern New Guinea, as *P. longipila* also.

Pygophora simplex Hennig, 1952

Pygophora simplex Hennig, 1952, *Beitr. Ent.* 2: 58. Holotype ♂, FLORES. In the Deutsches Entomologisches Institut, Berlin.

Diagnosis

Both sexes with several well developed *ad* setae, and usually with some small *pd* setulae, on the hind tibia in addition to the normal two strong *ad* and two strong *pd* setae (Fig. 19). ♂ hypopygium as in Fig. 94, ♀ T4 with a transverse row of distinct discal setae (as shown in Fig. 39).

Description

♂. *Head*: occiput pale grey pollinose. Frons slightly broader than in most species. Interfrontal area deep orange-yellow. Face, parafacials and parafrontals yellow pollinose. Ocellar setae well developed and about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellow-orange, third segment about 4.1 times as long as second segment and falling short of mouth-margin by about one-ninth of its length; arista long-plumose on basal two-fifths. Palpi yellowish-white. Mentum red-brown. *Thorax*: ground colour entirely blackish, humeral calli and mesonotum concolorous with rest of mesonotum; pleurae grey pollinose, dorsum yellowish-grey pollinose without trace of vittae. Presutural acrostichal hairs in a single, sometimes slightly irregular, row; *prst dc* seta not preceded by a *dc* setula; two *post ia* setae present. *Wings*: entirely hyaline. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for mid and hind coxae which are reddish-grey or blackish with pale grey pollinosity. Fore tibia with the *pv* seta about three-fifths as long as distance from its insertion to apex of tibia, and with two or three small *ad* setae. Mid femur with two preapical *p* setae, without special-

ised bristling, with three short fine *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the two *pd* setae about one and one and a half times as long as tibial diameter. Hind femur with two or three very short fine and inconspicuous *pv* setae; hind tibia without a preapical lobe or *pv* setae, but with four or five smaller *ad* setae in addition to the usual two strong *ad* setae (Fig. 19) and usually with some small semi-erect *pd* setulae in addition to the two strong *pd* setae, the *d* preapical seta short and only about half as long as hind metatarsus (the supernumerary setae and setulae give the hind tibia an unusually bristly appearance); hind tarsus simple. *Abdomen* (Fig. 61): of normal form, not noticeably laterally compressed, lobes of sternite 5 large. T1 + 2 and T3 almost entirely pale reddish-yellow, but T1 + 2 sometimes with a faint reddish-brown median vitta and T3 with faintly indicated reddish-brown sublateral spots and median vitta with some thin whitish pollinosity between the spots; T4 mainly dark in ground colour but reddish-yellow ventro-laterally and pale yellowish along dorsal hind margin, with grey pollinosity and with dark brown or blackish-brown median and sublateral spots (which are generally similar to those in the ♀, Fig. 39); T5 dark in ground colour dorsally but reddish-yellow ventro-laterally with greyish pollinosity and with dark brown sublateral spots and a dark brown median area, the latter less distinct than that on T4; T7 + 8 blackish-brown in ground colour with dense grey pollinosity but without spots; epandrium yellowish-orange with thin greyish-white pollinosity basally, the yellowish-orange colour noticeably contrasting with the dark T7 + 8. *Venter*, lobes of sternite 5 and paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, but the ventro-apical marginal setae of T5 very long and strong (Fig. 61). Hypopygium as in Fig. 94, paralobes with characteristic long slightly sinuous shape, each on the inner surface at the apex with a few minute blunt black spinules. *Measurements*: body length 4.0 mm (range 3.9 to 4.2 mm), wing length 3.5 mm (range 3.4 to 3.8 mm) [3 specimens].

♀. Generally similar to ♂ with the same supernumerary setae on the hind tibia, but antennae shorter, pollinosity of face, parafacials and parafrontals very pale yellow or yellowish-white, prescutum with a distinctly differentiated *dc* setula preceding the *prst dc* seta, and hind femur with three very long subequal *pv* setae in basal half. *Abdomen* (Fig. 39) with T1 + 2 entirely yellow, T3 mainly yellow or reddish-yellow but partly darkened in ground colour medio-dorsally with a pair of rounded or squarish dark brown sublateral spots and with a reddish brown median vitta, pale yellowish pollinose between the spots; T4 mainly dark in ground colour and pale yellowish pollinose (the tergite therefore appearing grey in colour), hind margin narrowly pale yellowish, with a pair of small slightly elongate blackish-brown sublateral spots and a blackish-brown median vitta; T5 similar to T4, appearing mainly grey (yellowish pollinose over a dark ground colour), with a pair of small blackish-brown sublateral spots but with only a faint trace of a median brown pollinose line, hind margin laterally pale yellowish; T3, T4 and T5 each with a lateral pair of large reddish or blackish-brown spots in addition to the markings on the dorsum. Generally grey appearance of last two tergites contrasting slightly with the predominantly yellowish colour of the two basal tergites. T4 with a transverse row of distinct erect discal setae and with the marginal setae very strong, T5 with several strong median discal setae. *Measurements*: body

length 4.7 mm (range 4.5 to 4.9 mm), wing length 4.1 mm (range 4.0 to 4.3 mm) [7 specimens].

Affinities

P. simplex is a small, rather isolated species, which is easily distinguished from other species by the extra bristles on the extensor surface of the hind tibia and by the unusual shape of the ♂ paralobes; the shape of the ♂ sternite 5 and the transverse row of discal setae on T4 in the ♀ are also characteristic. It does not appear to have any obvious close affinity with other species, but the small size and colouring is somewhat similar to that of *P. longipila* (Stein) and *P. enigma* sp. n.

Material examined

Paratypes: 4 ♂♂, 5 ♀♀, FLORES (Indonesia): Rana Mesé, 20–30.vi.1927 (*Sunda Expedition*) (D.Ent.Inst. and B.M.Nat.Hist.). JAVA: 1 ♀, Batavia, i.1908 (*E. Jacobson*) (Zool.Mus.Amsterdam). BURU (Indonesia): 1 ♀, Station 9, 29.vi.1921 (*L. J. Toxopeus*) (U.S.Nat.Mus.). DUTCH NEW GUINEA: 1 ♀, Vogelkop, Fak Fak, S. coast of Bomberai, 10–100 m., 11.vi.1959 (*T. C. Maa*) (Bishop Mus.). RYUKYU ISLANDS: 1 ♂, Ishigaki Island, 1–5.i.1953 (*G. E. Bohart*) (B.M.Nat.Hist.).

The specimen from Java in the Zoölogisch Museum, Amsterdam, bears Stein's determination label "Coenosia sp. b. tumidiventris Stein?", but the specimen certainly belongs to *P. simplex*; *P. tumidiventris* (Stein) belongs in a different group in which there is only one *p* preapical seta on mid femur.

Distribution

Known from the localities listed above and (Hennig, 1952) from Lombok (Serala, 20.iii.1927 (*Sunda Expedition*)) and Sumbawa (Sumbawa Bésar, 24.iv. to 2.v.1927 (*Sunda Expedition*)).

Pygophora liturata (Walker, 1864) **comb. n.**

Caenosia liturata Walker, 1864, *J. Proc. Linn. Soc.* 7: 218. Holotype ♀, MYSOŁ [= MISOÖL]. In the British Museum (Natural History), London.

Diagnosis

♂. Hypopygium as in Fig. 77, each paralobe with strong black teeth on inner edge (Fig. 92), hind femur with a row of four or five strong subequal *pv* setae in basal half (Fig. 28); fore tibia without *ad* setae in both sexes.

Description

♂. *Head*: occiput grey pollinose over blackish ground colour which contrasts with yellowish genae. Interfrontal area orange-yellow, bright orange immediately above lunula. Face whitish pollinose; parafacials and parafrontals bright yellow pollinose over yellow ground colour, parafrontals therefore not contrasting with interfrontal area. Ocellar setae short and fine but about equal in size to upper reclinate frontal setae which are hair-like. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae, the latter slightly more

widely spaced than usual. Antennae bright orange-yellow, third segment about 3.2 times as long as second segment and falling short of mouth-margin by about one-fifth of its length; arista plumose on basal two-fifths but hairs on ventral side short and inconspicuous. Palpi yellowish-white. Mentum reddish-brown. *Thorax*: ground colour blackish, humeral calli and scutellum concolorous with rest of mesonotum; dark grey pollinose, the pollinosity a little yellowish-grey on dorsum but mesonotum without vittae. Presutural acrostichal hairs in two rows, slightly irregular and close-set, but only a single median row just behind suture; no distinct *dc* setula preceding *prst dc* seta; two *post ia* setae present, the anterior one very fine. *Wings*: entirely hyaline. Calyptrae pale yellowish with yellowish-white fringes. Halteres pale yellow. *Legs*: yellow, including the coxae. Fore tibia without *ad* setae, the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia. Mid coxa with ventro-apical setae very fine; mid femur with two preapical *p* setae, *pv* surface with a very conspicuous short and strong submedian seta, setae of *av* row hair-like; mid tibia without an *ad* seta, the two *pd* setae about two and two and a half times as long as tibial diameter. Hind femur with four or five strong setae forming an obvious subequal row on basal half of *pv* surface (Fig. 28); hind tibia without a preapical lobe or *pv* setae, the *av* seta very small, the *d* preapical seta about half as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 77): slightly contracted towards the apex but not strongly laterally compressed, T5 not forming a keel, lateral lobes of sternite 5 large and leaf-like and very thin. T1 + 2 and sides of T3 reddish-yellow, T3 dorsally with some thin greyish-white pollinosity and a pair of reddish-brown sublateral spots and a diffuse median reddish area; T4 reddish-yellow ventro-laterally, otherwise brownish in ground colour with pale grey pollinosity, with red-brown median and sublateral spots; T5 mainly dark brownish in ground colour, only yellowish along ventral margins, pale grey pollinose with large reddish-brown median and sublateral spots widely separated by grey pollinose areas; T7 + 8 and epandrium reddish-brown with grey pollinosity, T7 + 8 with reddish-brown median and sublateral spots; the spots on T3 to T7 + 8 forming three obvious rows, the median ones tending to form a broad line. Venter and lobes of sternite 5 yellowish, but lobes of sternite 5 very thin and partly transparent, paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, ventro-apical marginal setae of T5 not very strongly developed. Hypopygium (Fig. 77) with acuminate paralobes, each with a ridge on the outer edge basally bearing several strong blunt black inwardly-directed teeth (Fig. 92), inner surface of paralobe medially also with strong black tooth-like processes. *Measurements*: body length 4.2 mm, wing length 3.8 mm [1 specimen].

♀. Generally very similar to ♂, but plumose hairs on ventral side of arista as long as those on upper side. Abdomen pale reddish-yellow on T1 + 2 and along hind margins of T3 and T4, otherwise dark in ground colour and grey pollinose, T3, T4 and T5 each with bold blackish-brown median and sublateral spots which form three distinct rows along the abdomen, the median spots of T3 and T4 very large elongate and parallel-sided and reaching anterior edges of the tergites, the sublateral spots smaller and more or less oval in shape (not extending round the sides of the tergites), T4 and T5 also with a pair of small blackish-brown ventro-

lateral spots which are less distinct than the spots on the dorsum. T4 without median discal setae, T5 with a pair of strong median discal setae standing on either side of the narrow blackish median line. Measurements: body length 4.6 mm, wing length 4.0 mm [1 specimen].

Affinities

The affinities of *P. liturata* are not clear: the ♂ hypopygium with its curious blunt black teeth is unlike that of any other species, and there are no other characters by which its relationships can be ascertained.

Material examined

Holotype ♀ [head missing], DUTCH NEW GUINEA: Mysol I. (= Misool), — (A. R. Wallace). INDONESIA: 1 ♂, Amboina, — (F. Muir) (B.M.Nat.Hist.); DUTCH NEW GUINEA: 1 ♀, Schouten Is., Biak I., Kampong Landbouw, 30 km. N.E. of air-strip, 40 m., 16.vii.1957 (D. E. Hardy) (B.M.Nat.Hist.).

Distribution

Known only from the three localities listed above and probably confined to the islands of eastern Indonesia and near the north-west tip of New Guinea.

Pygophora abnormala Paramonov, 1961

Pygophora abnormala Paramonov, 1961, *Ann. Mag. nat. Hist.* (13) 3: 508. Holotype ♂, AUSTRALIA. In the Division of Entomology Museum, C.S.I.R.O., Canberra.

Diagnosis

♂. Abdomen not flattened on T5, lateral lobe of sternite 5 as in Fig. 62. Dorsal preapical seta of hind tibia exceptionally long (about equal in length to hind metatarsus) and mid femur with dense setulae on apical quarter of *pv* surface.

Description

♂. *Head*: occiput pale grey pollinose. Interfrontal area orange-yellow. Face and parafacials pale yellowish-white pollinose. Ocellar setae much shorter and finer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange or pale yellowish-orange, third segment about twice as long as second segment (unusually short) and falling short of mouth-margin by about its own length or slightly more; arista long-plumose on basal two-fifths. Palpi yellowish-white [brownish on apical two-thirds in the holotype which is a teneral specimen]. Mentum yellow-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae densely pale grey pollinose; mesonotum and scutellum densely grey pollinose with hardly any trace of dark vittae. Presutural acrostichal hairs in two rows, developed as distinct setae; the *dc* setula preceding the *prst dc* very well developed; two distinct *post ia* setae present. *Wings*: entirely hyaline, without trace of apical dark suffusion. Calyptrae creamy-white with white fringes. Halteres yellow. *Legs*: entirely reddish-yellow except for mid and hind coxae which are partly dark reddish with grey pollinosity. Fore tibia with the *pv*

seta very short, only half as long as distance from its insertion to apex of tibia, and with two small *ad* setae. Mid femur with two preapical *p* setae, and with a row of dense *pv* setulae on apical quarter or third; mid tibia without an *ad* seta, the two *pd* setae only one and two times as long as tibial diameter. Hind femur with one very long submedian *pv* seta, the other *pv* setae very small; hind tibia without a preapical lobe, without *pv* setae, the *d* preapical seta unusually long and about equal in length to hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 62): T5 not laterally compressed so that the abdomen is not constricted in dorsal view, lateral lobes of sternite 5 shaped as in Fig. 62. T1 + 2 and T3 yellow with thin white pollinosity but without dark marks or with only a very small median dorsal red-brown spot on T3; T4 yellowish laterally and on the anterior and posterior margins dorsally, with dark red-brown sublateral spots and trace of a red-brown median spot, areas between the spots and outside the sublateral spots pale grey pollinose; T5 mainly dark in ground colour, only narrowly yellowish on dorso-apical margin, densely pale grey pollinose, with a pair of small but well marked blackish-brown sublateral spots but no median spot; T7 + 8 similar to T5 in colour but the lateral spots very small. Venter, lobes of sternite 5 and hypopygium reddish-yellow, T5 with a sparse row of long strong bristles on the ventro-apical margin and with a well developed row of marginal setae dorsally; T7 + 8 with a transverse row of strong dorsal setae and several weaker apical setae. *Measurements*: body length 6.25 mm (range 5.9 to 6.6 mm), wing length 5.7 mm (range 5.5 to 6.0 mm) [4 specimens].

♀. Generally similar to ♂ with the same short antennae, and with entirely yellow legs. Abdomen with T1 + 2 reddish-yellow; T3 reddish-yellow basally and apically but largely dark in ground colour, with blackish-brown median and sublateral spots, with the area around and between the spots yellowish-grey pollinose; T4 similar to T3 with small blackish-brown median and sublateral spots, but only narrowly reddish-yellow along apical margin behind the row of well developed marginal setae; T5 darkish in ground colour with dense yellow-grey pollinosity and very small sublateral spots but no median spot. Median spot of T4 rather indistinct and only half as long as the tergite and much smaller than the median spot of T3 or a sublateral spot of T4 (all spots generally rather smaller than in other species with abdominal spots). T4 without median discal setae. T5 with several erect discal setae irregularly arranged. Subapical *pv* setae of mid femur less dense than in male; *pv* surface of hind femur with three very long subequal setae in basal half. Mesonotum with distinct traces of yellowish-brown *dc* vittae. *Measurements*: body length 6.7, 6.8 mm, wing length 6.1, 6.1 mm [2 specimens].

Affinities

A distinctive species not very closely allied to other species, although the female is somewhat similar to that of the common Australian species *P. apicalis* Schiner.

Material examined

Holotype ♂, AUSTRALIA: New South Wales, Broadwater, xi.1927 (*D. S. North*). AUSTRALIA: 1 ♂, New South Wales, Sydney, 6.xi.1922 (*Health Dept.*) (*S.P.H.T.M.*); 1 ♀, New South Wales, Broadwater, xi.1927 (*E. G. Baber*) (*Div.Ent.Mus.Canberra*);

1 ♀, New South Wales, Sydney, Collaroy, 5.ix.1921 (*Health Dept.*) (U.S.Nat.Mus.);
 1 ♀, New South Wales, Botany Bay, (*H. Petersen*) (U.S.Nat.Mus., damaged);
 2 ♂♂, Queensland, Kuranda, (*Lichtwardt*) (B.M.Nat.Hist. and U.S.Nat.Mus.); 1 ♀,
 Woy Woy, 7.ix.1923 (*Mackerras*) (S.P.H.T.M.).

Distribution

Known only from eastern Australia, Queensland and New South Wales. The three ♀ specimens doubtfully assigned to *abnorma* by Paramonov (1961) are certainly conspecific with the ♂ holotype. One of the specimens has been examined.

Pygophora bakeri sp. n.

Note: This species was recognised as new by Malloch, who attached a type label to the single known male "Pygophora bakeri Det. J. R. Malloch type". This is an unpublished manuscript name. I am here describing the species, giving it the name chosen but not published by Malloch. Unfortunately the one male lacks the abdomen, but since the female is distinguishable from that of all other species a ♀ holotype has been designated. The male specimen still bears Malloch's M.S. label.

Diagnosis

♀ (? also ♂). Distinguished from all other known species by the presence on the abdomen of a pair of very strong erect median discal setae standing close together near the anterior margin of T4 (Fig. 37)*; antennae in both sexes extremely short. [♂ hypopygium and sternite 5 not known.]

Description

♀. *Head*: occiput greyish-white pollinose. Interfrontal area bright yellow becoming slightly yellowish-orange posteriorly. Face, parafacials, parafrontals and ocellar triangle with yellow ground colour and dense pollinosity which is silvery-white and brilliant in some lights but scarcely visible in others; parafrontals strongly contrasting with yellow interfrontal area when viewed so that the bright silvery-white pollinosity is fully visible. Ocellar setae much longer and stronger than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellow or pale orange-yellow, unusually short, third segment only a little more than twice as long as second segment and falling short of mouth-margin by about its own length or a little more, arista long-plumose on basal two-fifths. Palpi yellowish-white. Mentum reddish-brown. *Thorax*: ground colour entirely dark reddish-brown to blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae silvery-grey pollinose; mesonotum and scutellum clear grey pollinose, the mesonotum with distinct black *dc* vittae visible in some lights, the areas outside the *dc* rows of setae rather thinly pollinose so that to the naked eye the area of the mesonotum between the *dc* rows appears as a broad longitudinal grey band contrasting with darker areas laterally (especially obvious seen from behind). Presutural acrostichal hairs in two rows; no *dc* setula preceding *prst dc* seta; two *post ia* setae present, but anterior one small and fine. *Wings*: yellowish hyaline. Calyptrae white with white fringes. Halteres

* In *P. simplex* Hennig there is a pair of small fine median discals on T4 but these stand at the middle of the segment.

pale yellow. *Legs*: entirely yellow, including all coxae. Fore tibia with two *ad* setae. Mid femur with two preapical *p* setae and with the usual (♀) three long fine *pv* setae in basal three-fifths; mid tibia without an *ad* seta. Hind femur with three very long subequal *pv* setae in basal three-fifths; hind tibia without *pv* setae. *Abdomen* (Fig. 37): almost entirely dark in ground colour, only very narrowly pale on extreme hind margins of tergites, pale silvery-grey pollinose, T3, T4 and T5 with very distinct blackish-brown or dark reddish-brown sublateral and ventro-lateral spots, T3 and T4 also with very large subquadrate median black-brown spots, T1 + 2 with a large median dorsal subtriangular or subquadrate blackish-brown mark, T5 without trace of a median spot, the ventro-lateral dark spots clearly and widely separated from the sublateral spots by pollinose areas. T4 with a very strong pair of erect median discal setae standing close together on the median spot near the anterior margin, T5 also with a pair of strong median discal setae standing on the median pollinose area. *Measurements*: body length 5.9 mm. (range 5.6 to 6.2 mm), wing length 5.2 mm (range 5.0 to 5.4 mm) [6 specimens].

♂. Almost identical with ♀ [but abdomen and genitalia missing in only ♂ seen, ? T4 with median discal setae as in ♀]. Fore tibia with the *pv* seta erect and very fine, about three-quarters as long as distance from its insertion to apex of tibia; mid coxa and mid femur without specialised bristling; mid tibia with the two *pd* setae very long, the proximal one about four times and the distal one nearly six times as long as tibial diameter; hind femur with two very strong conspicuous *pv* setae in the middle third; hind tibia without a preapical lobe or *pv* setae, the *av* seta very strong, *d* preapical seta probably nearly as long as hind metatarsus [both hind tarsi missing in one ♂ seen]. Abdomen probably coloured much as in ♀. *Measurements*: body length (estimated as abdomen missing) 5.6 mm, wing length 5.0 mm [1 specimen].

Affinities

As the ♂ genitalia are not known it is not possible to deduce the affinities of *P. bakeri* sp. n. from this character; other characters give little clue to the affinities, but the very short antennae may suggest some relationship with the Australian species *P. abnormalis* Paramonov.

Material examined

Holotype ♀, PHILIPPINE ISLANDS: Luzon, Mt. Makiling, — (*Baker*). In the United States National Museum, Washington. Paratypes: 1 ♂, 6 ♀♀, same data as holotype (U.S.Nat.Mus. and B.M.Nat.Hist.); PHILIPPINE ISLANDS: 1 ♀, Mindanao, Butuan, — (*Baker*) (U.S.Nat.Mus.); 1 ♀, no data other than "Coll. Osten-Sacken" (D.Ent.Inst.).

Distribution

Only known from the above-listed material from the Philippines and probably an endemic species confined to this territory.

Pygophora unicolor (Stein, 1920) **comb. n.**

Coenosia unicolor Stein, 1920, *Tijdschr. Ent.* 62 Suppl.: 64. Holotype ♀, JAVA. In the Zoölogisch Museum, Amsterdam.

Diagnosis

Distinguished from all other species yet known by the entirely dark semi-shining blackish-brown colour.

Description

♀. *Head*: occiput thinly grey pollinose, dark ground colour clearly visible through the pollinosity. Interfrontal area velvety dark brown. Face thinly whitish pollinose, the dark reddish-brown ground colour showing through. Parafacials and lower parts of parafrontals silvery-white or creamy-white pollinose, upper parts of parafrontals thinly yellow pollinose. Ocellar setae very strong, about equal in size to *lower* reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae with second segment dark brown basally and laterally and with a contrasting yellow dorsal apex, third segment mainly brown but yellowish on basal half of inner surface, third segment about 2.5 times as long as second segment and falling short of mouth-margin by about half its length; arista long-plumose on basal half. Palpi brown or yellowish-brown, more yellowish at apices. Mentum dark red-brown. *Thorax*: unicolorous dark blackish-brown or very dark reddish-brown, semi-shining and with only very thin greyish pollinosity laterally, appearing black to naked eye. Presutural acrostichal hairs in two rows; a very distinct *dc* setula present in front of the *prst dc* seta; two *post ia* setae present. *Wings*: entirely hyaline. Calyptrae very pale lemon yellow with yellowish-white fringes. Halteres yellow. *Legs*: coxae dark reddish-brown, all femora very dark brown (only yellowish at extreme apices), tibiae and tarsi yellow or brownish-yellow. Fore tibia with one to three small *ad* setae. Mid femur with two preapical *p* setae and three very long *pv* setae in basal half; mid tibia without an *ad* seta. Hind femur with three very long subequal *pv* setae in basal half; hind tibia without *pv* setae. *Abdomen*: unicolorous shining very dark reddish-brown or blackish-brown, almost glossy black to naked eye. T4 and T5 without distinct median discal setae, marginal setae of T4 weak. *Measurements*: body length 5.0, 4.6 mm, wing length 4.3, 4.5 mm [2 specimens].

♂. Unknown. Probably general colour shining black-brown as ♀, but antennae probably much longer than in ♀. Hind tibia probably without preapical lobe, and legs probably without specialised bristling.

Affinities

P. unicolor is the only species of *Pygophora* which is entirely blackish-brown and more or less shining, and this unusual appearance makes it a distinctive species; in the absence of males, however, it is not possible to assess its affinities with other species.

Material examined

Holotype ♀, JAVA: Wonosobo, iv.1909 (*E. Jacobson*). MALAYA: 1 ♀, Pahang, Gunong Taban Padang, 5550 ft., 23.xii.1922 (*H. M. Pendlebury*) (B.M.Nat.Hist.).

S. INDIA: 3 ♀♀, Nilgiri Hills, Cherangode, 3500 ft., xi.1950 (*P. S. Nathan*) (B.M. Nat.Hist.); 1 ♀, Coorg, Ammatti, 3100 ft., x.1952 (*P. S. Nathan*) (B.M.Nat.Hist.). N.E. NEW GUINEA: 1 ♀, Kassam, 48 km. E. of Kainantu, 1350 m., 28.x.1959 (*T. C. Maa*) (Bishop Mus.).

Distribution

Known only from the above-named localities but possibly widespread in south-east Asia into Indonesia and New Guinea. The records suggest that *P. unicolor* may be a species of mountainous country: the type locality in Java lies at several thousand feet, and this is true of the other known localities.

***Pygophora xanthogaster* sp. n.**

Diagnosis

Very large species, ♀ distinguished from all other species by the unicolorous orange abdomen, which is devoid of spots or marking and contrasts with the greyish-black thorax.

Description

♀. *Head*: occiput densely pale grey pollinose. Interfrontal area reddish or brownish-orange. Face thinly whitish pollinose, the yellowish-brown ground colour showing through. Parafrontals yellow in ground colour with yellowish-white pollinosity, parafrontals darkish in ground colour with yellowish-white pollinosity but appearing very pale greyish. Ocellar setae well developed, about equal in size to upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange-yellow or brownish-yellow basally, third segment orange-yellow at the base but pale brownish on apical two-thirds, third segment about 3.6 times as long as second segment and falling short of mouth-margin by about half its length; arista long-plumose on basal half. Palpi yellow or pale yellow. Mentum orange-brown. *Thorax*: ground colour dark reddish-black laterally and almost black dorsally, the humeral calli concolorous with rest of mesonotum but scutellum slightly brownish apically; pleurae thinly greyish-white pollinose with the reddish-black ground colour more or less visible through the pollinosity, mesonotum mainly thinly grey pollinose but with distinct broad black *dc* vittae (especially visible when viewed from behind) and also with an indistinct median brownish pollinose vitta, the mesonotal pollinosity appearing yellowish-grey in certain lights. Presutural acrostichal hairs in three or four close-set slightly irregular rows; *prst dc* seta preceded by a very distinctly developed *dc* setula; two well developed *post ia* setae present (*post ia* hairs numerous and close-set in the holotype). *Wings*: slightly tinged with yellow, especially towards the anterior margins. Calyptrae very pale lemon yellow with yellowish-white fringes. Halteres pale orange-yellow. *Legs*: entirely orange-yellow except for bases of mid coxae which are reddish-black with pale grey pollinosity. Fore tibia with two or three small *ad* setae. Mid femur with two preapical *p* setae and with three strong but not very long subequal *pv* setae in basal three-fifths; mid tibia without an *ad* seta. Hind femur with three very long subequal *pv* setae in basal half; hind

tibia without *pv* setae. *Abdomen*: unicolorous shining or semi-shining orange or yellowish-orange, only T4 (in two dorsal longitudinal bands) and T5 (medially) showing a very thin trace of silvery or yellowish pollinosity, this pollinosity not imparting any evident pattern to the abdomen. T4 and T5 both without median discal setae, marginal setae of T4 weak with only the median marginal pair slightly erect and strong. *Measurements*: body length 7.0 mm (range 6.5 to 7.7 mm), wing length 6.4 mm (range 5.8 to 6.7 mm) [3 specimens].

♂. Unknown.

Affinities

P. xanthogaster differs from other known species in having a unicolorous orange abdomen (it may be presumed that this character is similar in the ♂) and in the large size. In the absence of the ♂, which is not yet known, its affinities with other species are not clear, but the pattern-less abdomen and absence of median discal setae on T5 suggest possible affinity with *P. unicolor* (Stein).

Material examined

Holotype ♀, CEYLON: Suduganga, 31.iii.1922 (—). In the British Museum (Natural History). Paratypes: 1 ♀, CEYLON: Suduganga, 6.viii.1920 (—) (B.M. Nat.Hist.); 1 ♀, CEYLON: —, — (Dr. Thwaites) (B.M.Nat.Hist.).

Distribution

Known only from Ceylon.

DIVISION B

Pygophora microchaeta sp. n.

Diagnosis

Basal pair of scutellar setae minute and hair-like, humeral calli yellow but scutellum blackish in ground colour, mid femur with one preapical *p* seta, ♂ hypopygium as in Fig. 75.

Description

♂. *Head*: occiput pale greyish-yellow pollinose. Interfrontal area yellow-orange. Face, parafacials, parafrontals and ocellar triangle pale yellowish pollinose. Ocellar setae small and very fine, very much finer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae pale orange, third segment about 2.75 times as long as second segment and falling short of mouth-margin by about three-fifths of its length; arista long-plumose on basal three-fifths. Palpi pale yellowish-white. Mentum dark yellowish-brown. *Thorax*: humeral calli yellow, rest of thorax including the scutellum blackish in ground colour; pleurae pale grey pollinose, mesonotum yellow-grey pollinose without vittae. Presutural acrostichal hairs in two irregular rows; *prst dc* seta not preceded by a small *dc* setula; only one small and very fine *post ia* seta present; basal pair of setae of the scutellum minute and represented only by a pair of hairs which are only slightly larger than those on the disc of the

scutellum. *Wings*: entirely hyaline. Calyptrae whitish with white fringes. Halteres pale reddish-yellow. *Legs*: entirely yellow, including the coxae. Fore tibia without distinct *ad* setae although there are a few very small *ad* setulae in the apical half which are but little larger than the tibial hairs, the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia. Mid coxa with the paired ventro-apical setae very strong and lying close together; mid femur with one preapical *p* seta, without specialised bristling, the *pv* surface with three long fine setae in the basal two-thirds; mid tibia without an *ad* seta, the two *pd* setae two and three times as long as the tibial diameter. Hind femur with three long *pv* setae of which the middle one is the longest; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta almost as long as hind metatarsus; hind tarsus simple. *Abdomen*: of normal subcylindrical form, not strongly laterally compressed but rather narrow and elongate, lateral lobes of sternite 5 large and shaped as in Fig. 75, each lobe with a ventral fringe of long very fine hairs. Tergites almost entirely pale reddish-orange or yellowish-orange with only thin traces of yellowish-white pollinosity visible in certain lights; all tergites without median spots, but T4 with a pair of very small indistinct brown sublateral spots and a pair of larger brown spots on the sides and T5 and T7 + 8 each with a pair of medium-sized oval dark reddish-brown sublateral spots. Venter reddish-yellow, lobes of sternite 5 pale semi-translucent yellow, paralobes of hypopygium shining yellow. Tergites without specialised bristling, marginal setae of sides of T5 fine. Hypopygium as in Fig. 75, paralobes narrow and slightly recurved, each with an area of small black spinules at the apex of the inner surface. *Measurements*: body length 4.8 mm, wing length 4.2 mm [1 specimen].

♀. Unknown.

Affinities

P. microchaeta is a curious species differing from all other known species in having the lateral scutellar setae reduced to a pair of small hair-like setulae; it is also unique in having the humeral calli yellow but the scutellum blackish (in other species if the humeral calli are yellow the scutellum is yellow also). The presence of only one preapical *p* seta on the mid femur, the lack of specialised bristling, and the form of the abdomen and hypopygium indicate general affinity with *P. lutescens* Frey and *P. nigromaculata* sp. n. as well as with the African species.

Material examined

Holotype ♂, INDIA: Assam, Doom Dooma (= Dum Duma), 1.v.1943 (*D. E. Hardy*). In the United States National Museum, Washington. Paratype ♂, same data as holotype, in the British Museum (Natural History).

Distribution

Known only from the material listed above from Assam.

Pygophora pendleburyi sp. n.*Diagnosis*

Very small species, mid femur with one preapical *p* seta, humeral calli and scutellum concolorous with mesonotum, fore tibia without *ad* setae; ♂ hypopygium and sternite 5 as in Fig. 76.

Description

♂. *Head*: occiput grey pollinose. Interfrontal area yellow. Face and parafacials whitish pollinose, parafrontals pale yellow pollinose. Ocellar setae very fine, about equal to or a little longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange-yellow, third segment paler than the others and about 2.75 times as long as second segment, falling short of mouth-margin by about a quarter of its length; arista long-plumose on basal half. Palpi pale yellow. Mentum orange-brown. *Thorax*: ground colour dark reddish-brown laterally and blackish dorsally (more brown on scutellum), humeral calli concolorous with mesonotum; pleurae grey pollinose, dorsum rather thinly greyish pollinose so that the ground colour is easily visible in some lights, especially the brownish colour of the scutellum, mesonotum without vittae but very narrow black *dc* lines visible from some angles. Presutural acrostichal hairs strong, in a single slightly irregular median row; no *dc* setula preceding *prst dc* seta; two *post ia* setae present but anterior one very small and fine intermediate in size between *ia* hairs and the definite second *ia* seta. *Wings*: entirely hyaline. Calyptrae yellowish-white with white fringes. Halteres pale yellow. *Legs*: entirely yellow, including all coxae. Fore tibia without *ad* setae, the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia. Mid femur with only one preapical *p* seta, without specialised bristling, with four long fine *pv* setae in basal two-thirds; mid tibia without an *ad* seta, the two *pd* setae about two and three times as long as tibial diameter. Hind femur with two very long strong *pv* setae in basal two-fifths; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta short and only about half as long as hind metatarsus; hind tarsus simple. *Abdomen*: expanded somewhat in the dorso-ventral plane so that the abdomen is deep towards the apex in lateral view, but not laterally compressed and T5 not forming a flattened dorsal keel, lateral lobes of sternite 5 as in Fig. 76. T1 + 2 and T3 entirely yellow; T4 only reddish-yellow ventro-laterally, dorsally mainly very dark semi-shining reddish-brown with traces of two grey thinly pollinose longitudinal lines (in the positions where the sublateral spots are normally separated from the median spot); T5 reddish-yellow ventro-laterally but elsewhere dark in ground colour with very large blackish-brown median and sublateral spots which occupy most of the dorsum of the tergite, the spots separated by thin grey pollinose lines; T7 + 8 blackish-brown in ground colour with grey pollinosity, with a very large blackish brown median and reddish-brown sublateral spots; epandrium dark reddish with thin grey pollinosity. Venter reddish-yellow, lateral lobes of sternite 5 shining semi-translucent yellow, paralobes of hypopygium yellow. Tergites without specialised bristling, lateral marginal setae of T5 long and strong but not strongly aggregated together ventro-apically. Hypopygium (Fig. 76) with small simple paralobes. *Measurements*: body length 3.8 mm, wing length 3.5 mm [1 specimen].

♀. Unknown. Probably generally very similar to ♂.

Affinities

P. pendleburyi appears to be closely related to the African species *P. parvipuncta* (Stein) and also possibly to *P. microchaeta* sp. n.; both these species have only one preapical posterior seta on the mid femur and a dark scutellum as in *pendleburyi*. *P. pendleburyi* is distinguishable from both species by the ♂ hypopygium and from *P. parvipuncta* by lacking the small *ad* setae on the fore tibiae; from *P. microchaeta* it differs in possessing the normal four strong bristles on the scutellum, and in having blackish humeral calli.

Material examined

Holotype ♂, MALAYA: Perak, Larut Hills, 3700–4000 ft., 11.ii.1932 (*H. M. Pendlebury*). In the British Museum (Natural History), London.

Distribution

Known only from the holotype from Malaya, but there is a ♀ *Pygophora* specimen which may belong to this species in the U.S.Nat.Mus. collection from Sumatra (Fort de Kock, 920 m., 1925 (*E. Jacobson*)).

Pygophora parvipuncta (Stein, 1906)

Coenosia parvipuncta Stein, 1906, *Berl. ent. Z.* 51: 77. Holotype ♂, TOGO REPUBLIC. In the Zoologisches Museum der Humboldt-Universität, Berlin.

Diagnosis

The only African species in which humeral calli and scutellum are blackish in ground colour and concolorous with rest of mesonotum; ♂ with an area of dense setulae at apex of *pv* surface of mid femur, paralobes of hypopygium as in Fig. 100.

Description

♂. *Head*: occiput pale greyish-white pollinose. Interfrontal area pale yellow. Face, parafacials and parafrontals very pale yellowish-white pollinose. Ocellar setae rather small, a little shorter than upper reclinate frontal setae. Parafrontals without supernumerary inclinate setae between upper and lower inclinate frontal setae. Antennae pale orange-yellow, third segment 2.75 times as long as second segment and falling short of mouth-margin by about half its length; arista long-plumose on basal half. Palpi creamy-white. Mentum yellowish-brown. *Thorax*: ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae pale greyish-white pollinose, mesonotum pale yellowish-grey pollinose without trace of vittae. Presutural acrostichal hairs in two rows; no differentiated *dc* setula preceding *prst dc* seta; only one distinct *post ia* seta present. *Wings*: entirely hyaline. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow, mid coxae slightly greyish basally. Fore tibia with the *pv* seta about three-fifths as long as distance from its insertion to apex of tibia, and with two or three small *ad* setae. Mid femur with one preapical *p* seta, *pv* surface with an area of dense setulae near the apex and with four long *pv*

setae in basal two-thirds, *av* surface without specialised bristling; mid tibia without an *ad* seta, the two *pd* setae one and two and a half times as long as tibial diameter. Hind femur with two long well separated submedian *pv* setae; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about two-thirds as long as hind metatarsus; hind tarsus simple. *Abdomen*: of normal cylindrical form, not laterally compressed, lobes of sternite 5 large and shaped as in Fig. 114, each lobe with a sparse ventral fringe of long hairs. T1 + 2 pale reddish-yellow with thin white pollinosity and with trace of darker median longitudinal line; T3 largely pale reddish-yellow with white pollinosity and with traces of darker ground colour dorsally and with a distinct median longitudinal brown line; T4 and T5 mainly dark in ground colour, only pale reddish-yellow on posterior margins, with pale greyish-white pollinosity, each with a pair of small dark brown sublateral spots but without median spots (although there is a faint yellow-brown pollinose median dorsal line); T7 + 8 brownish-black in ground colour with greyish-white pollinosity. Tergites without specialised bristling, T5 ventro-apically with four or five very strong marginal setae on either side. Venter, lobes of sternite 5, and paralobes of hypopygium reddish-orange. Hypopygium as in Fig. 100, each paralobe narrow and slightly recurved so that outer margin is slightly concave and with numerous short strong black spinules on outer surface of basal two-thirds; paralobe also with one isolated spinule on anterior edge near the apex. *Measurements*: body length 4.4 mm, wing length 3.9 mm [1 specimen].

♀. Closely similar to ♂ but all specimens seen with two or three very small hairs on parafrontals near the inclinate setae. Abdominal tergites with distinct blackish-brown median longitudinal vitta, T3 with a pair of small indistinct pale orange-brown sublateral spots, T4 with a large pair of dark orange-brown sublateral spots, T5 without distinct spots. T4 without median discal setae, T5 with a pair of median discal setae in addition to lateral discal setae. Mid femur without an area of dense *pv* setulae and mid and hind femur both with three long *pv* setae in basal two-thirds. *Measurements*: body length 4.6, 4.8 mm, wing length 3.8, 4.6 mm [2 specimens].

Affinities

Closely related to other African species but differing in the unicolorous dorsum of the thorax. *P. parvipuncta* also shows close affinities with the small Malayan species *P. pendleburyi* sp. n.; both species have only one preapical seta on the posterior surface of the mid femur, and the lobes of sternite 5 are very similar in shape, but the paralobes of the hypopygium and the colour and pattern of the abdomen are different.

Material examined

Holotype ♂, TOGO REPUBLIC: Bismarckburg, 15–21.xi.1892 (*L. Conradt*). LIBERIA: 1 ♀, Robertsport, 11.xi.1943 (*F. Snyder*) (U.S.Nat.Mus.); 1 ♀, —, 20.vi.1945 (*M. S. Briscoe*) (U.S.Nat.Mus.). CONGO: 1 ♂, 1 ♀, Katanga, Bianco, 8–11.viii.1931 (*J. Ogilvie*) (B.M.Nat.Hist.).

Distribution

Known only from the above-named localities in West and Central Africa, and

from Stein's (1918) record of a ♂ from Mujenje (in Uganda) (this specimen was formerly in Budapest Museum and was destroyed in 1956).

***Pygophora vittigera* sp. n.**

Diagnosis

Mid femur with one preapical *p* seta and yellow humeral calli and scutellum, ♂ abdomen with bold dark median vitta on first three tergites (Fig. 33), epandrium (T9) very enlarged with the orifice widely separated from T7 + 8, lateral lobes of sternite 5 small and shaped as in Fig. 59, hind femur with one very long submedian and a very small sub-basal *pv* seta.

Description

♂. *Head*: occiput pale greyish-white pollinose. Interfrontal area pale yellow. Face, parafacials, and parafrontals yellowish-white pollinose. Ocellar setae very small and fine, a little longer than upper reclinate frontal setae which are minute. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae very pale orange-yellow, very short, third segment only 1.8 times as long as second segment and falling short of mouth-margin by a distance almost equal to its length; arista long-plumose on basal two-thirds, the hairs unusually long. Palpi yellowish-white. Mentum yellow. *Thorax*: humeral calli and scutellum yellow in ground colour, paler than rest of mesonotum which is reddish-brown in ground colour, pleurae mainly reddish but propleural depressions and parts of pteropleura yellowish in ground colour; pleurae white pollinose, dorsum yellowish-white pollinose without trace of mesonotal vittae. Presutural acrostichal hairs in two rows; a very small *dc* setula differentiated in front of the *prst* *dc* seta; one small *post ia* seta present, the *ia* hairs very few in number. *Wings*: with a very faint yellowish tinge. Calyptrae yellowish-white with white fringes. Halteres pale creamy-yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with the *pv* seta about three-fifths as long as distance from its insertion to apex of tibia, and with one small distinct *ad* seta. Mid femur with one preapical *p* seta, without specialised bristling, with two or three long *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the two *pd* setae two or three times as long as tibial diameter. Hind femur with one very long submedian *pv* seta and with a very small *pv* seta between this and the base, the long seta over three times as long as the small one; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about three-fifths as long as hind metatarsus; hind tarsus simple. *Abdomen* (Figs. 33 and 59): of normal shape, not strongly laterally compressed, but epandrium (T9) very enlarged with the small orifice remote from T7 + 8 which is relatively small compared with the epandrium, lateral lobes of sternite 5 small and shaped as in Fig. 59, ventro-apically sternite 5 with a fringe of bristly hairs. T1 + 2 and T3 very pale yellowish and very thinly white pollinose, each with a large orange-brown median mark (which with the median dark mark of T4 and to a less extent of T5 forms a median longitudinal dark vitta on the dorsum of the abdomen); T4 mainly yellowish in ground colour but distinctly white pollinose dorsally with a large orange-brown median mark and with traces of small pale

orange-brown sublateral spots, laterally with a pair of well developed orange-brown spots against the anterior margin; T5 partly reddish-yellow in ground colour and yellowish-white pollinose, with a pair of very large dark brown sublateral spots and medially with traces of a narrow orange-brown line, on each side with a brown spot against the anterior margin (as shown in Fig. 59) similar to, but smaller than, that on T4; T7 + 8 yellowish-orange with some yellowish-white pollinosity and a pair of small brown sublateral spots; epandrium reddish-orange with very thin yellowish-white pollinosity. Tergites without specialised bristling, the ventro-apical marginal setae of T5 very weak, short and fine. Venter reddish-yellow, sternite 5 darkened basally and with translucent yellow lobes, paralobes of hypopygium reddish-orange. *Measurements*: body length 5.6 mm, wing length 5.0 mm [1 specimen].

♀. Closely similar to ♂ with the same very short antennae. Abdomen mainly pale reddish-yellow; T3 with a very narrow median brown line and without sublateral spots; T4 with partly dark ground colour dorsally, with a pair of blackish-brown sublateral spots and a less distinct narrow elongate median brown area (separated from the sublateral spots by greyish pollinose areas), laterally with a pair of brown spots against the anterior margin; T5 with a pair of small rounded dark brown sublateral spots and with a pair of brown spots on the sides against the anterior margin. T4 without median discal setae, T5 with a pair of very fine median discal setae. *Measurements*: body length 6.0 mm, wing length 5.3 mm [1 specimen].

Affinities

Belongs in the group of species characterised by possessing only one *p* preapical seta on mid femur and closely related to *P. lutescens* Frey and *P. pallens* (Stein) and also to *P. tumidiventris* (Stein); distinguished by the structure of the ♂ epandrium and sternite 5 and by the very short antennae.

Material examined

Holotype ♂, PHILIPPINE ISLANDS: Luzon, Mt. Makiling, — (Baker). In the United States National Museum, Washington. SARAWAK: 1 ♀, Kapit District, Merirai V., 30–300 m., 1–6.viii.1958 (*T. Maa*) (B.M.Nat.Hist.).

Distribution

Only known from the two specimens listed above.

Pygophora tumidiventris (Stein, 1904) **comb. n.**

Coenosia tumidiventris Stein, 1904, *Tijdschr. Ent.* 47: 112. Holotype ♂, JAVA. In the Zoölogisch Museum, Amsterdam.

Diagnosis

Mid femur with one preapical *p* seta, humeral calli and scutellum yellow, ♂ sternite 5 and hypopygium as in Figs. 106, 110, and 122.

Description

♂. *Head*: occiput densely whitish pollinose. Interfrontal area deep yellow. Face, parafacials and parafrontals pale yellowish-white pollinose. Ocellar setae fine, a little longer than upper reclinate frontal setae which are very small. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae with basal segments orange-yellow, third segment pale yellow and about 2.6 times as long as second segment, falling short of mouth-margin by about three-fifths of its length; arista long-plumose on most of its length, only the extreme tip bare. Palpi pale yellow. Mentum yellow. *Thorax*: humeral calli and scutellum yellow in ground colour and contrasting with blackish mesonotum, pleurae mainly reddish-brown in ground colour but yellowish in places on edges of the sclerites, pleurae greyish-white pollinose, dorsum pale yellowish pollinose. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a very small but clearly differentiated *dc* setula; only one very fine *post ia* seta present. *Wings*: hyaline with a very faint yellowish tinge. Calyptrae yellowish-white with yellowish-white fringes. Halteres pale yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with a few very small *ad* setae which are only indistinctly differentiated from the tibial hairs, the *pv* seta very fine and only half as long as distance from its insertion to apex of tibia. Mid femur with one preapical *p* seta, without specialised bristling, *pv* surface with three very long setae and a smaller seta near the base; mid tibia without an *ad* seta, the two *pd* setae two and three times as long as tibial diameter. Hind femur with a very long submedian *pv* seta and a smaller *pv* seta about half as long near the base; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta only about one-third as long as hind metatarsus; hind tarsus simple. *Abdomen*: of normal subcylindrical form [the basal ventral semi-shining hemispherical swelling described by Stein (original description) is an artifact due to parasitisation], not laterally compressed, lateral lobes of sternite 5 large and rounded with a ventral fringe of fine hairs (Fig. 110) and the sternite deeply cleft in ventral view (Fig. 122). All tergites predominantly pale reddish-yellow with only very thin yellowish pollinosity, T1 + 2 and T3 without spots or markings; T4 with a pair of small red-brown sublateral spots and a pair of reddish-brown ventro-lateral spots; T5 with a pair of large reddish-brown sublateral spots and a less distinct narrow longitudinal median reddish-brown mark, also with an indistinct pair of brownish ventro-lateral spots visible in certain lights; T7 + 8 with distinct rounded orange-brown sublateral spots and a very indistinct median brownish area; epandrium reddish-yellow. Venter, lobes of sternite 5, and paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, lateral marginal setae of T5 long and fine but not forming a close-set ventro-apical row. Hypopygium as in Fig. 106, paralobes very slightly recurved. *Measurements*: body length 5.75 mm, wing length 5.1 mm [1 specimen].

♀. Unknown, probably almost identical with the ♀ of *P. lutescens*.

Affinities

Very closely allied to *P. lutescens* and *P. vittigera* and to other species of the group in which there is only one posterior preapical seta on the mid femur and in which the humeral calli and scutellum are yellowish.

Material examined

Holotype ♂, JAVA: —, — (Piepers). JAVA: 1 ♂, Sindaglaija, 4000—4500 ft., — (F. Muir) (B.M.Nat.Hist.).

Distribution

Known only from the material listed above from Java.

Pygophora pallens (Stein, 1915) **comb. n.**

Coenosia pallens Stein, 1915, *Suppl. ent. Berl.* 4: 52. Lectotype ♂, FORMOSA. In the Deutsches Entomologisches Institut, Berlin.

Lectotype designation: Stein described *C. pallens* from several specimens from Formosa. The ♂ syntype from Kosempo (in D.Ent.Inst.) has been selected and labelled as lectotype. The remaining syntypes have been labelled as paralectotypes.

Diagnosis

One preapical *p* seta on mid femur, humeral calli and scutellum yellow, ♂ abdomen short and deep and unusually broad in dorsal view (Fig. 35), hypopygium as in Fig. 105.

Description

♂. *Head:* occiput white pollinose over pale yellowish-grey ground colour. Interfrontal area pale yellow. Face, parafacials and parafrontals white pollinose over pale yellow ground colour. Ocellar setae longer than upper reclinate frontal setae which are very small. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae pale yellow, third segment short, about 2.3 times as long as second segment and falling short of mouth-margin by about three-quarters of its length; arista long plumose on basal half or three-fifths. Palpi creamy-white. Mentum yellow. *Thorax:* humeral calli, scutellum and edges of mesonotum yellow, parts of pteropleura, sternopleura and mesopleura extensively pale reddish-yellow in ground colour, other parts of pleura reddish-grey in ground colour and median area of mesonotum dark greyish or blackish in ground colour; pleurae white pollinose, mesonotum pale yellowish pollinose without trace of vittae. Presutural acrostichal hairs in one (sometimes slightly irregular) median row; *dc* setula preceding *prst dc* seta only very slightly differentiated; one *post ia* seta present. *Wings:* entirely hyaline. Calyptrae yellowish-white with yellowish-white fringes. Halteres pale yellow. *Legs:* entirely yellow including the coxae. Fore tibia with the *pv* seta very short, only half as long as distance from its insertion to apex of tibia, and with two or three small, sometimes indistinct, *ad* setae or setulae. Mid femur with one preapical *p* seta, without specialised bristling, with four long *pv* setae in basal two-thirds; mid tibia without an *ad* seta, the two *pd* setae one and a half and two times as long as tibial diameter. Hind femur with three long *pv* setae in basal three-fifths; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about three-fifths as long as hind

metatarsus; hind tarsus simple. *Abdomen*: short and unusually broad in dorsal view (Fig. 35), not laterally compressed, in side view deep (similar to *pallipalpis*, Fig. 72), lateral lobes of sternite 5 as in Fig. 115. T1 + 2 and T3 yellow, each with a trace of a darker orange or orange-brown median longitudinal mark; T4 and T5 predominantly yellowish or reddish-yellow, sometimes partly blackish in ground colour dorsally, each with a pair of orange-brown to blackish-brown sublateral spots and a longitudinal reddish-brown or blackish-brown median mark, areas between median and sublateral spots distinctly yellowish-white or greyish pollinose; T7 + 8 predominantly reddish-orange, sometimes partly dark greyish in ground colour antero-dorsally, with a distinct pair of sublateral spots and traces of a median reddish-brown mark; epandrium reddish-orange. Venter reddish-yellow, lobes of sternite 5 and paralobes of hypopygium yellowish. Tergites without specialised bristling, marginal row of T7 (apparent discal setae of T7 + 8) containing eight to ten setae. Hypopygium as in Fig. 105, epandrium unusually large, paralobes narrow and with some black setulae on inner surfaces. *Measurements*: body length 4.9 mm (range 4.7 to 5.1 mm), wing length 4.7 mm (range 4.5 to 4.9 mm) [6 specimens].

♀. Generally similar to ♂ but ground colour of sides of thorax usually less extensively yellowish. Abdomen predominantly reddish-yellow, T3, T4 and T5 each with a pair of bold rounded orange-brown to dark brown sublateral spots; T3 and T4 each with a large dark brown or orange-brown median mark, T5 with a narrow dark median line. T4 without median discal setae, T5 with a pair of strong median discal setae. Abdominal spots well separated from one another by pollinose areas and sublateral spots not very large, less than half as long as tergite; ventro-laterally T2–T5 with large reddish-brown areas. Measurements: body length 5.5 mm (range 5.3 to 5.7 mm), wing length 5.1 mm (range 4.9 to 5.2 mm) [7 specimens].

Affinities

Allied to other species in which there is only one preapical *p* seta on mid femur and in which the humeral calli and scutellum are yellow. It is most closely allied to *P. lutescens* Frey but is distinguishable by the unusually bulbous ♂ abdomen, by the shape of the lobes of sternite 5 and by the large epandrium; the shape of the paralobes also differs slightly. The more developed dark spots of the abdomen distinguish the ♀ from *lutescens*.

Material examined

Lectotype ♂, FORMOSA: Kosempo, v.1912 (*H. Sauter*). Paralectotypes: 5 ♂♂, 5 ♀♀, FORMOSA: Takao, 29.iii and 2.iv.1907 (*H. Sauter*) (Zool.Mus.Humb.Univ.); paralectotypes: 1 ♂, 1 ♀, FORMOSA: Takao, 29.iii.1907 (*H. Sauter*) (B.M.Nat.Hist.); paralectotype ♀, FORMOSA: Sokutsu, vi.1912 (*H. Sauter*) (D.Ent.Inst.). FORMOSA: 1 ♀, Tappani, 7.iv.1910 (*H. Sauter*) (D.Ent.Inst.); 1 ♀, no other data (D.Ent.Inst.). THAILAND: 2 ♂♂, 2 ♀♀, N.W. Thailand, Chiangmai Province, Chaingdao, 450 m., 5–11.iv.1958 (*T. C. Maa*) (one of the ♀♀ labelled *J. L. Gressitt*) (B.M.Nat.Hist. and Bishop Mus.); 1 ♂, Chiangmai, Fang, 500 m., 12–19.iv.1958 (*T. C. Maa*) (Bishop Mus.); 1 ♂, Chiangmai, Doi Suthep, 1278 m., 29.iii. to 4.v.1958 (*T. C. Maa*) (Bishop Mus.).

Distribution

Known from Formosa and Thailand. In addition to the Formosan localities listed above Stein (1915, 1918) and Hennig (1941) list *pallens* from Lambeh, Taihorinsho, Taihorin and Hoozan, but I have not seen material from these places.

Pygophora nigromaculata* sp. n.Diagnosis*

Mid femur with one preapical *p* seta and humeral calli and scutellum yellow, ♂ sternite 5 very enlarged with lateral lobe shaped as in Fig. 60, ♀ abdominal pattern as in Fig. 38.

Description

♂. *Head*: occiput yellowish-white pollinose over greyish ground colour. Interfrontal area deep orange-yellow. Face, parafacials and parafrontals yellowish-white pollinose. Ocellar setae well developed, much longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae pale orange-yellow, third segment 2.5 times as long as second segment and falling short of mouth-margin by about half its length; arista long-plumose on basal half. Palpi white. Mentum yellow. *Thorax*: humeral calli and scutellum yellow in ground colour, contrasting with rest of mesonotum which is blackish in ground colour, sides of thorax reddish-black with pale grey pollinosity; mesonotum pale yellowish pollinose without vittae. Presutural acrostichal hairs in two rows; *prst dc* seta preceded by a very small but clearly differentiated *dc* setula; one *post ia* seta present. *Wings*: entirely hyaline. Calyptrae very pale yellow with yellowish-white fringes. Halteres pale yellow. *Legs*: entirely yellow except for extreme bases of mid coxae which are narrowly blackish. Fore tibia with the *pv* seta about two-thirds as long as distance from its insertion to apex of tibia, and with only one clearly differentiated very small *ad* seta. Mid femur with one preapical *p* seta, without specialised bristling, with two long subequal *pv* setae in basal half and one smaller *pv* seta in basal part of apical half; mid tibia without an *ad* seta, the two *pd* setae one and a half and two times as long as tibial diameter. Hind femur with two *pv* setae in basal half, the first (basal) one about half as long as second; hind tibia without preapical lobe or *pv* setae, the *d* preapical seta about three-fifths as long as hind metatarsus; hind tarsus simple. *Abdomen* (Fig. 60): of normal form, not strongly laterally compressed, sternite 5 very large with broad lateral lobes shaped as in Fig. 60. T1 + 2 and T3 reddish-yellow, each with large median dorsal red-brown mark; T4 partly reddish-yellow latero-ventrally, dorsally with large bold black-brown median and sublateral spots narrowly separated by grey-pollinose areas; T5 reddish-yellow latero-ventrally, dorsally with a pair of large rounded almost black sublateral spots a smaller median black-brown mark (smaller and less distinct than that on T4), areas between the spots and laterally outside the sublateral spots whitish pollinose; T7 + 8 reddish in ground colour with bold black-brown sublateral spots but with only an indistinct dark median area, white pollinose except on the spots; epandrium yellowish-orange. Venter mainly reddish-yellow, lobes of sternite 5

yellow, paralobes of hypopygium translucent yellow. Tergites without specialised bristling, setae on ventro-apical margins of T5 not very strongly developed. Hypopygium as in Fig. 60, paralobes narrow and acuminate at the apices, inner posterior margin of each towards the apex with a short fringe of black setulae. *Measurements*: body length 5.2 mm, wing length 5.1 mm [1 specimen].

♀. Generally similar to ♂ except for abdominal pattern. Abdomen (Fig. 38) yellow or orange-yellow with a bold pattern as follows: T1 + 2 with a large median reddish-brown mark; T3 with a large red-brown median area formed of coalesced median and sublateral spots, the dark area with two longitudinal narrow thinly greyish pollinose lines visible in certain lights; T4 with a similar large median red-brown or dark brown area, but the dark area more distinctly formed of median and sublateral spots well separated by more definite pale pollinose areas; T5 with a pair of large dark brown sublateral spots; T4 without median discal setae, T5 with a pair of median discal setae standing between the sublateral spots. T3–T5 laterally each with a large red-brown mark. *Measurements*: body length 5.75 mm (range 5.3 to 6.2 mm), wing length 5.6 mm (range 5.2 to 5.9 mm) [8 specimens].

Affinities

P. nigromaculata belongs to the group of species in which there is only one preapical seta on the posterior surface of the mid femur and in which the humeral calli and scutellum are yellow, and is allied to *P. lutescens* and other Asiatic species of this group. The form of the ♂ sternite 5 and paralobes also suggests fairly close affinity with the African species *P. acromiata*.

Material examined

Holotype ♂, BURMA: N.E. Burma, Kambaiti, 7000 ft., 18.v.1934 (*R. Malaise*). In the British Museum (Natural History), London. Paratypes: 1 ♂, THAILAND: N.W. Thailand, Chiangmai, Fang, 500 m., 12–19.iv.1958 (*T. C. Maa*) (Bishop Mus.); 15 ♀♀, same locality and collector as holotype, dates 18.iv. to 7.vi.1934 (B.M.Nat.Hist.).

Distribution

Only known from the Burmese and Thailand localities listed above.

Pygophora lutescens Frey, 1917

Pygophora lutescens Frey, 1917, *Öfvers. finska VetenskSoc. Forh.* 59: 17. Holotype ♀, CEYLON. In the Museum Zoologicum Universitatis, Helsinki.

Diagnosis

One preapical *p* seta on mid femur and yellow humeral calli and scutellum, ♂ with lateral lobe of sternite 5 as in Fig. 111, and hypopygium as in Fig. 104.

Description

♂. *Head*: occiput yellowish-white pollinose. Interfrontal area yellow. Face, parafacials and parafrontals pale yellowish-white pollinose. Ocellar setae very fine, longer than upper reclinate frontal setae. Parafrontals without supernumerary

setae between upper and lower inclinate frontal setae. Antennae pale orange-yellow, third segment about 2.4 times as long as second segment and falling short of mouth-margin by about half its length; arista long-plumose on basal half. Palpi yellowish-white. Mentum yellow. *Thorax*: humeral calli and scutellum yellow in ground colour, not concolorous with rest of mesonotum which is dark brownish in ground colour, pleurae reddish-brown in ground colour; pleurae yellowish-white pollinose, mesonotum densely pale yellow pollinose without trace of vittae. Presutural acrostichal hairs in two rows; *prst dc* seta not preceded by a clearly differentiated *dc* setula; one *post ia* seta present. *Wings*: with a very faint yellowish tinge. Calyptrae yellowish-white with yellowish-white fringes. Halteres pale yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with the *pv* seta about three-fifths as long as distance from its insertion to apex of tibia, and with some very small *ad* setae. Mid femur with one preapical *p* seta, without specialised bristling; mid tibia without an *ad* seta, the two *pd* setae about one and a half and two times as long as tibial diameter. Hind femur with three long *pv* setae in basal two-thirds; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta much shorter than hind metatarsus; hind tarsus simple. *Abdomen*: of normal shape, not laterally compressed, lateral lobes of sternite 5 large and rounded (not very strongly acuminate) dorso-apically with ventral margins fringed with fine hairs (Fig. 111). T1 + 2 and T3 luteous yellow; T4 mainly yellowish with a pair of reddish-brown sublateral spots; T5 yellowish with a pair of blackish-brown sublateral spots and traces of a median dark area, pale greyish-white pollinose between median dark area and sublateral spots; T7 + 8 yellowish-red with a pair of small brown sublateral spots; epandrium reddish-yellow. Venter, lobes of sternite 5, and paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, T5 with the ventro-apical marginal setae very strong. Hypopygium as in Fig. 104, inner surface of each paralobe near the apex with some very short blunt black spinules. *Measurements*: body length 6.0 mm, wing length 5.4 mm [1 specimen].

♀. Generally similar to ♂, but antennae very short, ocellar setae very small, and thorax more densely yellow pollinose. Abdomen luteous or reddish-yellow, T3, T4 and T5 each with a pair of small rounded orange-brown or red-brown sublateral spots (those on T3 sometimes indistinct), but with little or no trace of darker median marks. T4 without median discal setae, T5 with a pair of weak median discal setae. *Measurements*: body length 5.3, 5.8 mm, wing length 4.8, 5.1 mm [2 specimens].

Affinities

P. lutescens belongs in the group in which there is only one preapical posterior seta on the mid femur and in which the humeral calli and scutellum are yellowish, and is most closely allied to *P. nigromaculata* sp. n. and *P. pallens* (Stein) from both of which it can be distinguished in the ♂ by the form of the sternite 5 and in the ♀ by the abdominal markings (as given in the key).

Material examined

Holotype ♀ [teneral specimen] CEYLON: Anuradhapura, 19-21.xii.1910 (*A. Luther*). CEYLON: 1 ♀, Maskeliya, 22.i.1919 (*G.D.A.*) (B.M.Nat.Hist.); 2 ♀♀, —, —,

1882 (*Stamforth Green*) (Oxf. Univ. Mus.). INDIA: 1 ♂, Mysore, Amabidacool Estate, 4400 ft., 25.iii. to 29.iv.1913 (*P.S.*) (B.M.Nat.Hist.); 1 ♀, Mysore, Herikanmuth, 2.xii.1915 (*T. V. Subramaniam*) (U.S.Nat.Mus.). In addition to the above-mentioned material I have seen two other females which may belong to *lutescens* but in which the abdominal pattern approaches that of *pallens*. These two specimens have the following data: Assam, Duamara, 2.xii.1943 (*D. E. Hardy*) (U.S.Nat. Mus.) and Ceylon (*Horn*) (D.Ent.Inst.). The head is missing in the latter specimen.

Distribution

Only certainly known from Ceylon and southern India, but possibly more widespread in south-east Asia.

Pygophora alemella Séguy, 1938

Pygophora alemella Séguy, 1938, *Mém. Mus. Hist. nat. Paris* (N.S.) 8: 368. Holotype ♂, KENYA. In the Muséum National d'Histoire Naturelle, Paris.

Diagnosis

African species with yellow humeral calli and scutellum, *prst dc* seta inserted on anterior half of prescutum about in line with *ph* seta (Fig. 30), ♂ with paralobes of hypopygium reddish-yellow and curved forwards (Fig. 102).

Description

♂. *Head*: occiput white pollinose, the grey ground colour showing through. Interfrontal area yellow. Face, parafacials and parafrontals white pollinose. Ocellar setae longer but finer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange-yellow basally, third segment pale yellow and about 2.6 times as long as second segment, falling short of mouth-margin by about half its length; arista long-plumose on basal three-fifths. Palpi white. Mentum yellow. *Thorax*: humeral calli and scutellum yellow in ground colour, contrasting with dark greyish pleurae and blackish dorsum; thoracic pollinosity white laterally and yellowish on dark areas of mesonotum. Presutural acrostichal hairs very small, in three or four irregular rows; *prst dc* seta extremely strong, inserted before middle of prescutum and about in line with *ph* seta, not preceded by a differentiated *dc* setula (Fig. 30); only one distinct *post ia* seta present. *Wings*: entirely hyaline. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with *pv* seta short, about half as long as distance from its insertion to apex of tibia, with two small *ad* setae. Mid femur with one preapical *p* seta, without specialised bristling, with three long *pv* setae in basal three-fifths of which middle one is longest; mid tibia without an *ad* seta, the two *pd* setae two and three times as long as tibial diameter. Hind femur with two *pv* setae in basal half of which the apical one is the longer; hind tibia without preapical lobe or *pv* setae, the *d* preapical seta about half as long as hind metatarsus; hind tarsus simple. *Abdomen*: of normal cylindrical form, not laterally compressed, lateral lobes of sternite 5 large but not strongly acuminate dorso-apically (Fig. 112).

Tergites mainly reddish-yellow with thin white pollinosity, T3 and T4 with faint traces of a reddish-brown median mark, T5 with a pair of distinct reddish-brown sublateral spots but without median spot, T7 + 8 with an indistinct pair of small brownish sublateral spots. Venter, lobes of sternite 5, and paralobes of hypopygium reddish-yellow. Tergites without specialised bristling, ventro-apical margins of T5 with only very weak marginal setae. Hypopygium as in Fig. 102, paralobes narrow and curved forwards with the exterior margin convex, each paralobe on inner surface of apical half with numerous very small blunt black socketed spicules. *Measurements*: body length 5.1 mm, wing length 4.6 mm [1 specimen].

♀. Closely similar to ♂, but all specimens seen with one or two minute hairs on parafrontals between upper and lower inclinate frontal setae. Abdomen with T4 sometimes partly blackish in ground colour and sometimes with a small indistinct pair of brown sublateral spots, T5 with a well developed pair of brown sublateral spots. T4 without median discal setae, T5 with a pair of strong median discal setae between the lateral discal setae standing on the sublateral spots. *Measurements*: body length 5.9 mm (range 5.7 to 6.1 mm), wing length 5.5 mm (range 5.4 to 5.5 mm) [4 specimens].

Affinities

P. alemella is very closely related to the other African species in which the humeral calli and scutellum are yellow in ground colour, viz. *P. acromiata* (Speiser) and *P. africana* sp. n. It differs from both these species in the structure of the hypopygium and in the noticeably forward position of the presutural dorsocentral seta.

Material examined

Holotype ♂, KENYA: Elgon Saw-Mill, Mt. Elgon ver'est (Camp II), 2470 metres, xii.1932 (C. Arambourg, P.-A. Chappins, and R. Jeannel). UGANDA: 1 ♂, 1 ♀, Ruwenzori Range, Nyamgasani Valley, 6400 ft., xii.1934 to i.1935 (D. R. Buxton) (B.M.Nat.Hist.); 2 ♀♀, Ruwenzori Range, Namwamba Valley, 6500 ft., xii.1934 to i.1935 (F. W. Edwards) (B.M.Nat.Hist.); 1 ♀, Ruwenzori Range, Kilembi, 4500 ft., xii.1934 to i.1935 (F. W. Edwards) (B.M.Nat.Hist.); 2 ♂♂, 2 ♀♀, Budongo Forest, 7-8.ii.1935 (F. W. Edwards) (B.M.Nat.Hist.).

In addition to the material listed above, there is in the B.M. a specimen (♀) in which there is a strong pair of frontal setae between the upper and lower pairs of inclinate frontal setae and a second well developed pair of presutural dorso-central setae *behind* the usual pair of *prst dc* setae. I am not certain that this specimen (from Budongo Forest, full data as above) is true *alemella*.

Distribution

An African species known from Kenya and Uganda. Specimens I have seen from West Africa closely resembling *P. alemella* belong to the very closely allied new species, *P. africana* sp. n.

Pygophora africana* sp. n.Diagnosis*

African species with yellow humeral calli and scutellum, *prst dc* seta inserted distinctly behind level of *ph* seta, ♂ mid femur without dense *pv* setulae, ♂ hypopygium with paralobes as in Fig. 103.

Description

♂. *Head*: occiput white pollinose. Interfrontal area orange-yellow. Face yellowish-white pollinose, parafacials and parafrontals pale yellow pollinose. Ocellar setae strong, appreciably longer than upper reclinate frontal setae. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae orange-yellow, third segment 2.9 times as long as second segment and falling short of mouth-margin by about three-fifths of its length; arista long-plumose on basal half. Palpi pale yellowish. Mentum yellow. *Thorax*: humeral calli and scutellum pale yellow in ground colour, paler than rest of dorsum which is brownish in ground colour, pleurae mostly pale reddish-grey in ground colour but largely pale yellowish in propleural depressions and on pteropleura; thoracic pollinosity whitish laterally and pale yellowish on dorsum. Presutural acrostichal hairs in three rows; *prst dc* seta inserted slightly nearer to transverse suture than to anterior margin of prescutum and distinctly behind level of *ph* seta, preceded by a small but clearly differentiated *dc* setula (Fig. 31); only one *post ia* seta present. *Wings*: very faintly yellowish tinged. Calyptrae pale yellowish-white with white fringes. Halteres very pale creamy-yellow. *Legs*: entirely yellow, including the coxae. Fore tibia with *pv* seta about two-thirds as long as distance from its insertion to apex of tibia, and with two *ad* setae. Mid femur with one preapical *p* seta, without specialised bristling, with four long subequal *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the *pd* setae two and three times as long as tibial diameter (holotype with a strong third *pd* seta between the normal two on left side). Hind femur with three long *pv* setae in basal three-fifths of which middle one is longest and about twice as long as basal one; hind tibia without preapical lobe or *pv* setae, the *d* preapical seta about half as long as hind metatarsus; hind tarsus simple. *Abdomen*: of normal form, not laterally compressed, lateral lobes of sternite 5 large and acuminate dorso-apically (closely similar to *P. acromiata*, Fig. 113). Tergites mainly yellow with very thin indistinct white pollinosity, T3 and T4 with a very faint trace of a darker yellow-brown median longitudinal line, T5 with a pair of yellowish-brown sublateral spots. Venter and lobes of sternite 5 yellow, paralobes of hypopygium dark shining brown. Epanthrium pale reddish-orange. Tergites without specialised bristling, ventro-apical margins of T5 with moderately strong marginal setae. Hypopygium as in Fig. 103, paralobes narrow and very slightly curved backwards, the apices slightly expanded and rounded (not pointed as in *acromiata*) with a few minute blunt spinules on inner surface. *Measurements*: body length 6.3, 6.9 mm, wing length 5.8, 5.9 mm [2 specimens].

♀. Closely similar to ♂ but thorax slightly darker in ground colour, propleural depressions and pteropleura not partly yellowish, and with four rows of *acr* hairs. Small *dc* setula before the *prst dc* seta less developed than in ♂. Abdomen with

T4 and T5 largely blackish in ground colour, T4 with extensive orange-brown median suffusion and with small red-brown sublateral spots, T5 with a pair of distinct brown sublateral spots; T1 + 2 with a median longitudinal pale orange-brown line. T4 without median discal setae, T5 with a pair of strong median discal setae between the lateral discal setae which stand on the sublateral spots. Measurements: body length 5.5 mm (range 5.2 to 5.7 mm), wing length 5.0 mm (range 4.7 to 5.2 mm) [3 specimens].

Affinities

Closely related to *P. acromiata* (Speiser) and *P. alemella* Séguy. The ♂ of *africana* is distinguished from both these species by the form of the paralobes of the hypopygium, and from *acromiata* also by lacking the dense irregular *pv* setulae on the mid femur. Both sexes may also be distinguished from *alemella* by the normal position of the *prst dc* seta which is inserted distinctly behind the level of the *ph* seta (in *alemella* the *prst dc* seta is inserted well forward on the prescutum about in line with the *ph* seta). *P. africana* differs from *P. parvipuncta* (Stein) in having yellowish humeral calli and scutellum.

Material examined

Holotype ♂, SIERRA LEONE: "Hill Station", 5.xii.1924 (*E. Hargreaves*). In the British Museum (Natural History), London. LIBERIA: 1 ♀, —, 25.x.1944 (*M. S. Briscoe*) (U.S.Nat.Mus.). GHANA: 1 ♀, Ashanti, Obuasi, 28.vii.1907 (*W. M. Graham*) (B.M.Nat.Hist.). TOGO REPUBLIC: 1 ♂, Bismarckburg, 3–10.xii.1892 (*L. Conradt*) (Zool.Mus. Humb.Univ.). N. NIGERIA: 1 ♀, Benue Province, Ibi, Benue River, 23.x.1909 (*H. A. Foy*) (B.M.Nat.Hist.).

Distribution

As yet only known from the above-named localities in West Africa from Sierra Leone to Nigeria. The male specimen from Togo was referred to by Stein (1906, p. 78) at the time when he described *P. humeralis* (Stein) (*acromiata* Speiser).

Pygophora acromiata (Speiser, 1910)

Coenosia humeralis Stein, 1906, *Berl. ent. Z.* 51: 77. Lectotype ♂, TANGANYIKA. In the Zoologisches Museum der Humboldt-Universität, Berlin.

Coenosia acromiata Speiser, 1910, in Sjöstedt: *Wiss. Ergeb. Schwed. zool. Exped. Kilimandjaro-Meru*, 10 (5): 159 (footnote). Nomen novum for *Coenosia humeralis* Stein, 1906, preoccupied by *Coenosia humeralis* Wiedemann, 1830.

Lectotype designation: *C. humeralis* was based on two ♂ and four ♀ syntypes from Tanganyika ("Nyassa-See") and one ♀ syntype from N. Cameroons. One of the ♂ syntypes has been selected and labelled as lectotype, and the remaining syntypes have been labelled as paralectotypes.

Diagnosis

African species with yellow humeral calli and scutellum and ♂ with dense irregular setulae on apical third of *pv* surface of mid femur and with strong shining black acuminate paralobes.

Description

♂. *Head*: occiput whitish pollinose. Interfrontal area lemon yellow. Face, parafacials and parafrontals white or pale yellowish-white pollinose. Ocellar setae about equal in size to upper reclinate frontal setae or a little longer. Parafrontals without supernumerary setae between upper and lower inclinate frontal setae. Antennae yellow, third segment about 2.6 times as long as second segment and falling short of mouth-margin by about two-thirds of its length; arista long-plumose on basal half. Palpi pale yellow. Mentum deep yellow. *Thorax*: humeral calli and scutellum light reddish-yellow in ground colour, not concolorous with rest of mesonotum which is blackish in ground colour, pleurae dark reddish-grey in ground colour; thoracic pollinosity whitish laterally and pale yellow dorsally, mesonotum without vittae. Presutural acrostichal hairs in two or three irregular rows; *dc* setula preceding *prst dc* seta only weakly differentiated; only one *post ia* seta present. *Wings*: entirely hyaline or with a very faint yellowish tinge. Calyptrae white with white fringes. Halteres pale yellow. *Legs*: entirely yellow except for bases of mid coxae which are reddish-black with grey pollinosity. Fore tibia with *pv* seta about two-thirds as long as distance from its insertion to apex of tibia, and with two small *ad* setae. Mid femur with one preapical *p* seta, *pv* surface with three long setae in basal half and with irregular rows of dense setulae in apical third (Fig. 12); mid tibia without an *ad* seta, the two *pd* setae one and a half and three times as long as tibial diameter. Hind femur with two long *pv* setae in basal half; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about two-thirds as long as hind metatarsus; hind tarsus simple. *Abdomen*: of normal form, not strongly laterally compressed, lateral lobes of sternite 5 large and acuminate dorso-apically (Fig. 113), each lobe with a ventral fringe of weak hairs. T1 + 2 and T3 yellow or pale reddish-yellow with only thin traces of white pollinosity, T3 sometimes with a darker yellow or brownish median longitudinal mark; T4 largely dark in ground colour antero-dorsally, reddish-yellow apically and ventro-laterally, with white pollinosity laterally and yellowish pollinosity dorsally and with two distinct red-brown sublateral spots and an indistinct median thinly pollinose reddish-brown mark; T5 similar to T4 but the sublateral spots larger and darker brown and median dark area very indistinct; T7 + 8 largely reddish-yellow, only darkish in ground colour antero-dorsally, with a pair of small brown sublateral spots and dense yellow-grey pollinosity dorsally; epandrium reddish-orange or reddish-yellow. Venter and lobes of sternite 5 reddish-yellow, paralobes of hypopygium shining black. Tergites without specialised bristling, lateral marginal setae of T5 rather weak, T5 usually with a pair of strong median discal setae between the sublateral spots (in addition to the lateral discal setae standing on outer edges of sublateral spots). Hypopygium as in Fig. 101, paralobes narrow, acuminate at the apices and slightly and evenly recurved, very strongly sclerotized, apically with a few very blunt thick spinules on inner surfaces. *Measurements*: body length 6.6 mm (range 6.4 to 7.0 mm), wing length 5.9 mm (range 5.7 to 6.3 mm) [6 specimens].

♀. Generally similar to ♂ but mid femur without dense *pv* setulae. Abdomen somewhat variable in colouring, T1 + 2 and T3 usually almost entirely yellow as in ♂, but sometimes T3 darkish on the dorsum; T4 and T5 largely darkish

red-brown or yellowish-brown in ground colour, usually only reddish-yellow on apical thirds, each with a pair of well developed red-brown, orange-brown or dark brown sublateral spots, T4 in addition with a median longitudinal non-pollinose red-brown area, otherwise both tergites yellowish-white pollinose. T4 without median discal setae, T5 with a pair of very strong median discal setae standing between the sublateral spots. Measurements: body length 6.8 mm (range 6.3 to 7.8 mm), wing length 6.0 mm (range 5.6 to 6.7 mm) [16 specimens].

Affinities

P. acromiata is closely allied to the other African species with yellow humeral calli and scutellum (*alemella* and *africana*) but is distinguished from both by the dense *pv* setulae of mid femur and the paralobes of the ♂. It also shows some affinity with the Burmese species *P. nigromaculata* sp. n. in which the form of the ♂ sternite 5 and hypopygium is very similar.

Material examined

Lectotype ♂, TANGANYIKA: Langenburg, Lake Nyasa, iii-iv.1898 (*S. G. Fülleborn*). Paralectotypes: 1 ♂, 4 ♀♀, data as for lectotype, and paralectotype ♀, CAMEROONS: Johann-Albrechtshöhe, 17.ix.1896 (*L. Conradt*) (all in Zool.Mus.Humb. Univ.). GHANA: 1 ♀, Ashanti, Obuasi, 5.vii.1907 (*W. M. Graham*); 1 ♀, Ashanti, Obuasi, 7.vii.1907 (*W. M. Graham*) (U.S.Nat.Mus.); 1 ♀, N. Territories, Makongo, 15.ii.1913 (*J. J. Simpson*). NIGERIA: 1 ♀ Lagos, 6.i.1910 (*A. Connal*) (U.S.Nat.Mus.); 1 ♀, Badagri, 10-12.xi.1911 (*L. E. H. Humfrey*); 2 ♂♂, 1 ♀, Abo, x.1911 (*J. W. S. Macfie*); 1 ♀, Zungeru, xi.1910 (*J. W. S. Macfie*). RUANDA-URUNDI: 1 ♂, Ruhengeri, 1900 m., 27.i.1953 (*P. Basilewsky*) (Mus.R.Afr.Cent.Tervuren); 1 ♀, Muhavura, contref.Est, 2100m., 28.i.1953 (*P. Basilewsky*) (Mus.R.Afr.Cent.Tervuren); 1 ♀, Kisenyi, Kayove, 2000 m., 14.ii.1953 (*P. Basilewsky*) (Mus.R.Afr.Cent.Tervuren). UGANDA: 1 ♂, 1 ♀, Ruwenzori Range, Kilembe, 4500 ft., xii.1934 to i.1935 (*F. W. Edwards*); 1 ♂, Semliki Valley, Buamba Forest, 2300-2800 ft., 3-7.xi.1911 (*S. A. Neave*); 1 ♂, Kigezi, Kayonza Forest, v-vi.1957 (*van Someren*); 1 ♂, Unyoro, Bugoma, 3700 ft., vii.1914 (*C. A. Wiggins*) (Oxf.U. Mus.). KENYA: 1 ♀, Ruiru, 6.vii.1932 (*H.C.J.*); 1 ♂, Ruiru, 13.vii.1932 (*H.C.J.*); 1 ♂, 1 ♀, Ruiru, 15.vii.1932 (*H.C.J.*); 1 ♂, Ruiru, 19.viii.1932 (*H.C.J.*); 1 ♂, Embu, Rugendo's 4400 ft., 14.vi.1914 (*J. O. Browne*). NYASALAND: 1 ♀, Cholo,—(*R.C. Wood*). MOZAMBIQUE: 1 ♀, E. of Mt. Mlanje, 3-7.x.1913 (*S. A. Neave*).

All the above listed material in the British Museum (Natural History) unless otherwise stated.

Distribution

Widespread in Africa from West Africa eastwards to Kenya and southwards to northern Mozambique. Emden (1956) also records the approximate distribution of this species.

Pygophora pallipalpis (Stein, 1910)

Coenosia pallipalpis Stein, 1910, *Trans. Linn. Soc. Lond. (Zool.)* Ser. 2 14: 160. Lectotype ♂, SEYCHELLES. In the British Museum (Natural History), London.

Lectotype designation: Stein described *Coenosia pallipalpis* from two ♂ and several ("mehrere") ♀ specimens. One of the ♂ syntypes is in the B.M.Nat.Hist. and has been selected and labelled as lectotype; the whereabouts of the other ♂ syntype is unknown. Two ♀ syntypes in B.M.Nat.Hist. and two ♀ syntypes in Zool.Mus. Humb.Univ. have been labelled as paralectotypes.

Diagnosis

Parafrontals with a few setulose hairs between lower inclinate frontal setae and eye-margins and with two pairs of supernumerary inclinate frontal setae, only one *p* preapical seta on mid femur.

Description

♂. *Head:* occiput pale grey pollinose. Interfrontal area deep velvety yellow-orange. Face and parafacials white pollinose, parafrontals and lunula silvery-white pollinose (strongly contrasting with yellow-orange interfrontal area). Ocellar setae strong, much longer than upper reclinate frontal setae. Parafrontals with two pairs of supernumerary inclinate setae between the upper and lower pairs of inclinate frontal setae, and each parafrontal between lower inclinate frontal seta and eye-margin with a few setulose hairs (Fig. 8). Antennae pale orange, third segment about 2.7 times as long as second segment and falling short of mouth-margin by nearly half its length; arista long-plumose on basal two-fifths. Palpi creamy-white. Mentum dark yellowish-brown or dark brown. *Thorax:* ground colour entirely blackish, humeral calli and scutellum concolorous with rest of mesonotum; pleurae grey pollinose, dorsum partly greyish pollinose laterally but mainly pale yellowish-brown pollinose (lectotype from Seychelles with traces of dark *dc* vittae in certain lights and with pale grey pollinosity between the *dc* rows of setae). Acrostichal hairs in four or five irregular rows, sometimes only in two rows on posterior part of prescutum; prescutum with unusually many hairs in front of the *ph* and *prst dc* setae, but no definite *dc* setula differentiated in front of the *prst dc* seta; *post ia* hairs more numerous than usual but only one (very strong) *post ia* seta present. *Wings:* entirely hyaline. Calyptrae whitish or pale creamy-yellowish with pale yellowish-white fringes. Halteres pale creamy-yellow. *Legs:* entirely yellow except for mid and hind coxae which are partly or mostly reddish-grey with white pollinosity. Fore tibia with two very small inconspicuous *ad* setae (sometimes only one evident), the *pv* seta fine and about two-thirds or three-quarters as long as distance from its insertion to apex of tibia. Mid femur with one preapical *p* seta, without specialised bristling, with four subequal *pv* setae in basal three-fifths; mid tibia without an *ad* seta, the two *pd* setae about one and a half and two times as long as tibial diameter. Hind femur with three long *pv* setae in basal two-thirds; hind tibia without a preapical lobe or *pv* setae, the *d* preapical seta about three-quarters as long as hind metatarsus which is rather short; hind tarsus simple. *Abdomen* (Fig. 72): rather deep in lateral view but not strongly laterally compressed, lateral lobes of sternite 5 not very large

but long and tapering, acuminate apically. All tergites mainly dark in ground colour and densely greyish, greyish-yellow or pale yellowish-brown pollinose, only extreme hind margins of each tergite very narrowly and inconspicuously pale yellowish-white; lectotype ♂ from Seychelles with a pair of large bold black sub-lateral spots on each tergite (largest on T4 and T5, least conspicuous on T1 + 2) but black spots only well developed on T5 in Madagascar material (spots absent on T1 + 2 and T3 and at most very small and inconspicuous on T4 and T7 + 8 in Madagascar specimens); tergites without median spots but abdomen on its whole length with at least faint trace of a narrow yellowish-brown pollinose median dorsal vitta; epandrium reddish-yellow and contrasting strongly with dark T7 + 8 in Madagascar material, but darker reddish-brown with pale grey pollinosity in lectotype. Sternites dark greyish medially and narrowly pale yellowish laterally, lobes of sternite 5 pale translucent yellow, paralobes of hypopygium shining reddish or reddish-yellow. Tergites without specialised bristling, but ventro-apical marginal setae of T5 strong. Hypopygium with very long and very narrow slightly recurved paralobes. *Measurements*: body length 5.4 mm (range 5.1 to 5.7 mm), wing length 5.0 mm (range 4.8 to 5.1 mm) [5 specimens].

♀. Generally similar to ♂, but setulose hairs on lower parafrontals stronger and more numerous, setulose hairs of prescutum also very numerous. Abdomen as in ♂ mainly dark in ground colour with dense greyish, or yellowish-grey, sometimes pale yellowish-brown pollinosity; pattern slightly variable, in some Madagascar specimens there are no spots but others show a pair of large black spots on T4 and sometimes less well developed spots on T3 and T5 also; Seychelles specimens with large well developed spots on all tergites; median dark pollinose vitta variable, sometimes distinct, sometimes virtually absent. T4 without median discal setae, T5 with median discal setae and with a very close-set row of unusually numerous fine apical marginal setae. *Measurements*: body length 5.7 mm (range 5.0 to 6.1 mm), wing length 5.2 mm (range 4.7 to 5.5 mm) [10 specimens].

Affinities

Generally related to other species in which there is only one preapical seta on the posterior surface of the mid femur and in which the paralobes of the ♂ hypopygium are long and narrow, but easily distinguished by the setulose lower parafrontals and two pairs of supernumerary inclinate frontal setae.

Material examined

Lectotype ♂, SEYCHELLES: Mahé, 1908-09 (*J. S. Gardiner*). Paralectotypes: 4 ♀♀, data as for lectotype. MADAGASCAR: Central Madagascar: 2 ♀♀, Tananarive, Tananarive, 20.x.1957 (*F. Keiser*); 2 ♀♀, Tananarive, Tananarive, 1.ix.1958 (*F. Keiser*); 1 ♀, Tananarive, Tananarive, 19.x.1958 (*F. Keiser*) (B.M.Nat.Hist.); 1 ♀, Tananarive, Analavory, 30.iii.1958 (*F. Keiser*); 2 ♀♀, Tananarive, Ampefy, 29.iii.1958 (*F. Keiser*) (one in B.M.Nat.Hist.). Eastern Madagascar: 2 ♂♂, 10 ♀♀, Tamatave, Perinet, 24.ix. to 8.x.1958 (*F. Keiser*) (1 ♂, 1 ♀ in B.M.Nat.Hist.); 1 ♂, 3 ♀♀, Tamatave, Tamatave, 27.x.1957 (*F. Keiser*) (1 ♀ in B.M.Nat.Hist.); 1 ♀, Tamatave, Foulpointe, 2.xi.1957 (*F. Keiser*); 1 ♀, Tamatave, Soanierana-Ivongo, 10.xi.1957 (*F. Keiser*); 1 ♀, Tamatave, Maroantsetra, 4.v.1958 (*F. Keiser*);

1 ♂, 3 ♀♀, Tamatave, Fampanambo, 29.iv.1958 (*F. Keiser*) (1 ♀ in B.M.Nat.Hist.); 1 ♀, Fianarantsoa, Vohiparara, 15.ix.1958 (*F. Keiser*); 1 ♀, Fianarantsoa, Ambatolahy, 14.ix.1958 (*F. Keiser*); 1 ♀, Fianarantsoa, Ranomafana, 3.viii.1958 (*F. Keiser*); 3 ♀♀, Fianarantsoa, Ifanadiana, 23–24.viii.1958 (*F. Keiser*) (1 ♀ in B.M.Nat.Hist.); 2 ♂♂, 7 ♀♀, Fianarantsoa, Mananjary, 7–21.viii.1958 (*F. Keiser*) (1 ♂, 1 ♀ in B.M.Nat.Hist.); 1 ♂, Fianarantsoa, Marofody, 18.viii.1958 (*F. Keiser*). Nosy Bé Island: 1 ♀, Ambalafar, 18.v.1958 (*F. Keiser*).

All above-listed Madagascar material is in Nat.Mus.Basel except where stated to be in B.M.Nat.Hist.

Distribution and discussion

Until recently *P. pallipalpis* (Stein) was known only from the type series collected on the Seychelles islands in 1908–09, but in the course of a visit to the Naturhistorisches Museum, Basel, I was surprised to find a good series of this species amongst the muscid material collected by Dr. Fred Keiser in Madagascar. Hitherto the genus *Pygophora* was unknown from the Malagasy Region. The Madagascar material shows the several remarkable characters found in the type series from the Seychelles, notably the curious setulose hairs on the lower parafrontals (not found in any other species of *Pygophora* known to me), the two pairs of supernumerary inclinate frontal setae, the single *p* preapical seta of the mid femur, and identical ♂ hypopygium and sternite 5, and there is no doubt that the Madagascar material is assignable to *P. pallipalpis*. There are, however, some differences in the abdominal pattern and pollinosity between the type series from Seychelles and the new material from Madagascar and it is possible that two good allopatric subspecies are involved. In the absence of a really good series from the Seychelles and lacking material from islands between Seychelles and Madagascar it seems best for the present not to describe the Madagascar form as a new subspecies. Nevertheless it will be useful to indicate the differences that do exist between the Seychelles type series and the Madagascar material:

Abdomen in both sexes with large bold black sublateral spots on each tergite, median dark pollinose vitta distinct, general pollinosity greyish; ♂ epandrium more or less reddish-brown with greyish pollinosity, not very noticeably contrasting with dark T7 + 8; thorax with traces of narrow blackish *dc* vittae in certain lights.....Seychelles form

Abdomen in both sexes only with one well developed pair of black sublateral spots (on T5 in ♂, T4 in ♀), at most only with traces of such spots on other tergites, in ♀ abdomen sometimes devoid of spots, general pollinosity usually rather yellowish with the darker narrow median vitta only very faintly indicated; ♂ epandrium reddish-yellow and noticeably contrasting in colour with dark T7 + 8; thorax without trace of dark *dc* vittae.....Madagascar form

Finally it may be noted that *P. pallipalpis* is recorded by Bezzi (1923) in his list of the Diptera of the Seychelles and is keyed out with the African mainland species by Emden (1940); *pallipalpis* was first placed in the genus *Pygophora* by Emden, *op. cit.*, p. 242.

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I am most sincerely grateful to the following specialists for their kindness in lending me type specimens and other material for study: Dr P. Basilewsky, Dr M. Beier, Mr J. E. Collin, Dr G. L. van Eynhoven, Dr R. H. Foote, Dr R. Frey, Mademoiselle Dr D. Guiglia, Dr W. Hackman, Dr W. Hennig, Dr F. Keiser, Dr K. H. L. Key, Dr E. Kjellander, Dr G. Kruseman, Mr D. J. Lee, Mr D. K. McAlpine, Dr A. Neboiss, Dr S. J. Paramonov, Dr F. Peus, Dr L. W. Quate, Professor E. Séguy, and Dr. S. L. Tuxen.

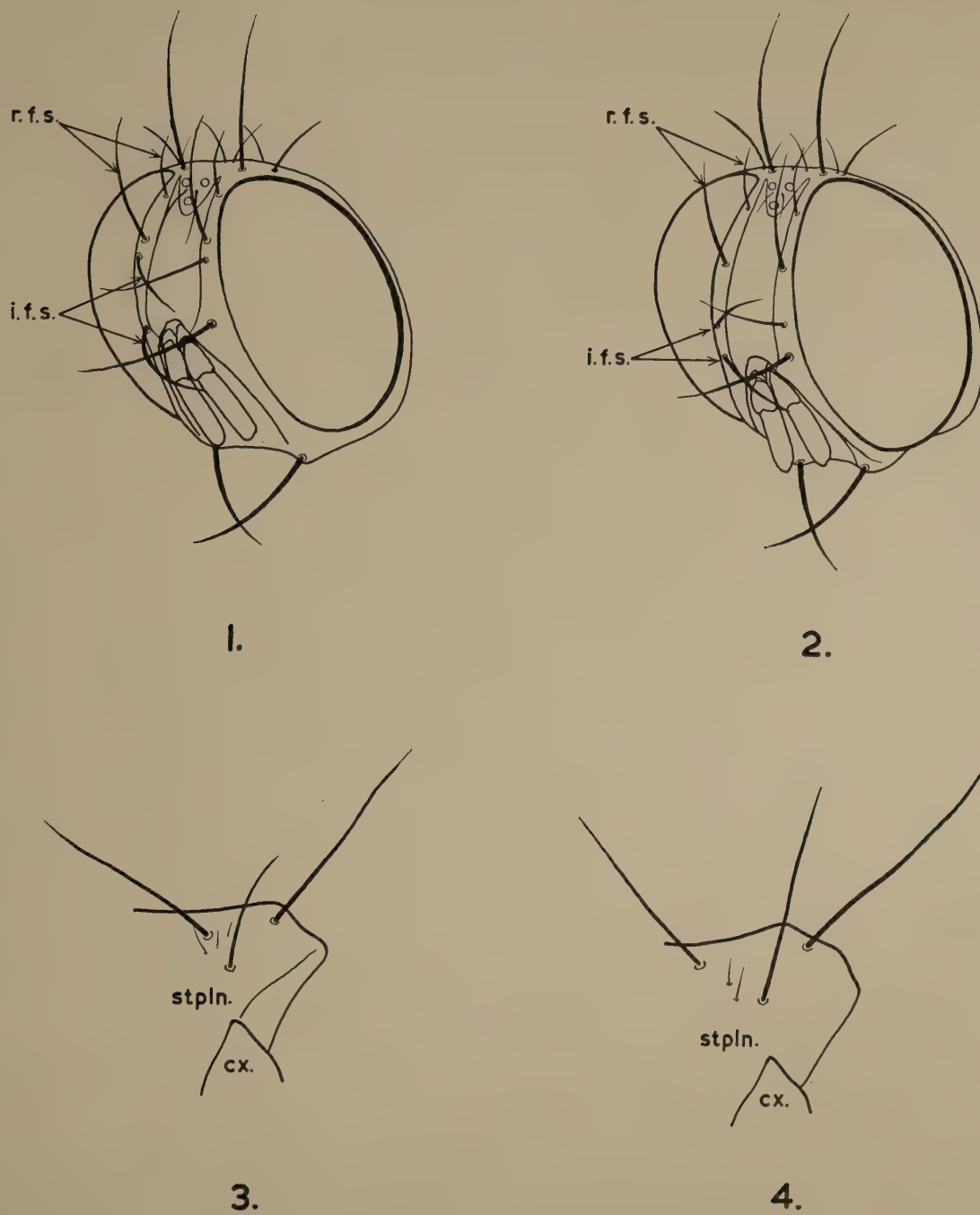
In addition I should like to thank Dr. L. W. Quate for examining and reporting on a type specimen in the Bernice P. Bishop Museum, Honolulu; and to Dr F. Mihályi of the Hungarian National Museum, Budapest, for confirming that some syntypes formerly in that collection have certainly been destroyed.

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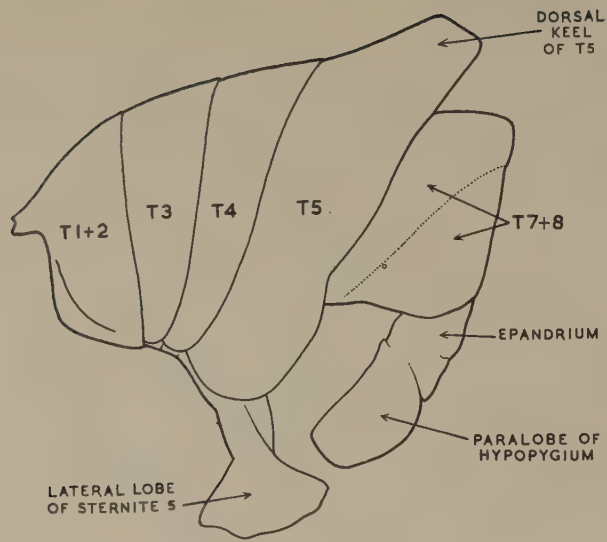
FIGURES 1-124
ON PAGES 527-549



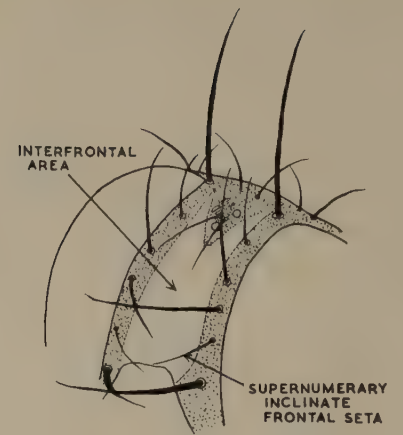
FIGURES 1-4

Fig. 1. Head of *Pygophora* Schiner. Fig. 2. Head of *Cephalispa* Malloch. Fig. 3. Sternopleural setae of *Pygophora*. Fig. 4. Sternopleural setae of *Cephalispa*.

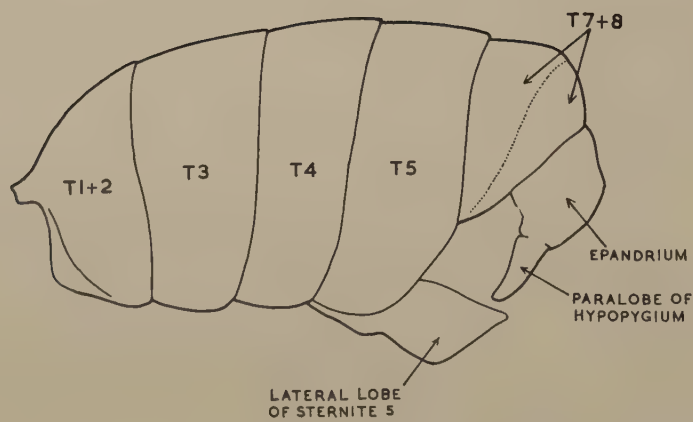
r.f.s. = reclinate frontal setae; *i.f.s.* = inclinate frontal setae; *stpln.* = sternopleuron; *cx.* = mid coxa.



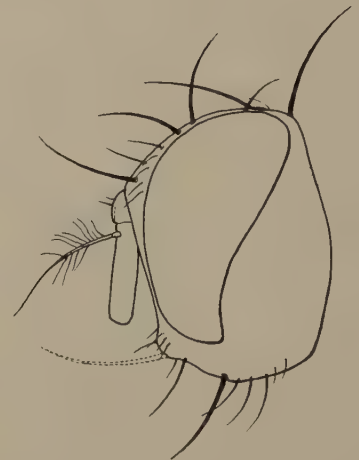
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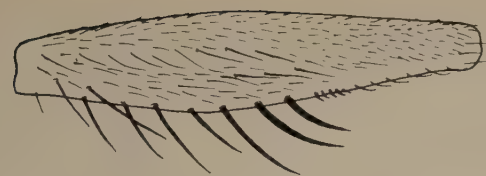


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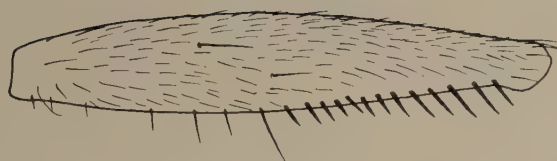
FIGURES 5-8

Fig. 5, 6. Different forms of abdomen in *Pygophora*. Fig. 7. Frontal area of head of species of *Pygophora* possessing a supernumerary pair of inclinate frontal setae. Fig. 8. Head of *P. pallipalpis* (Stein) in lateral view.

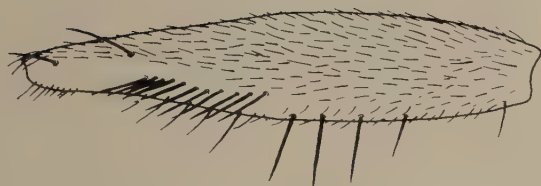
T = tergite.



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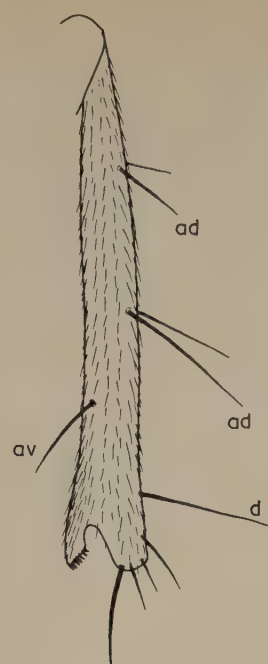
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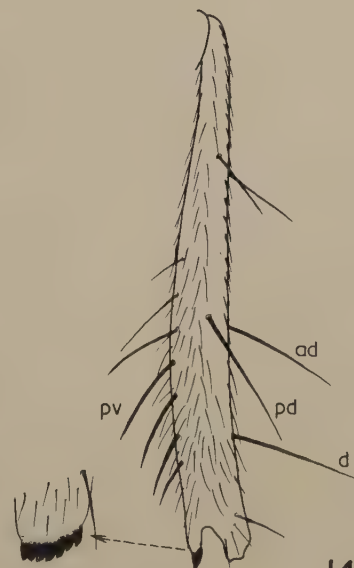
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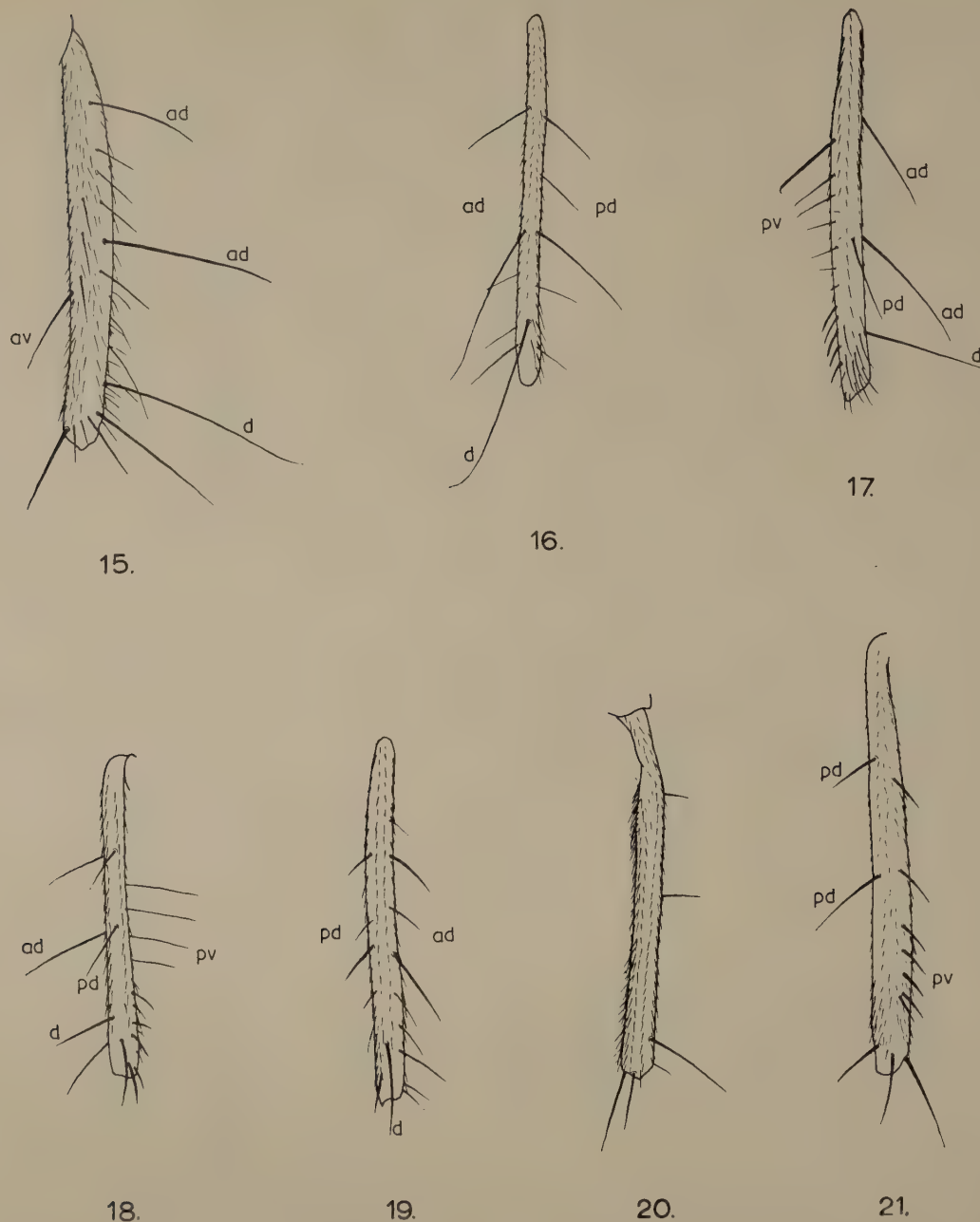
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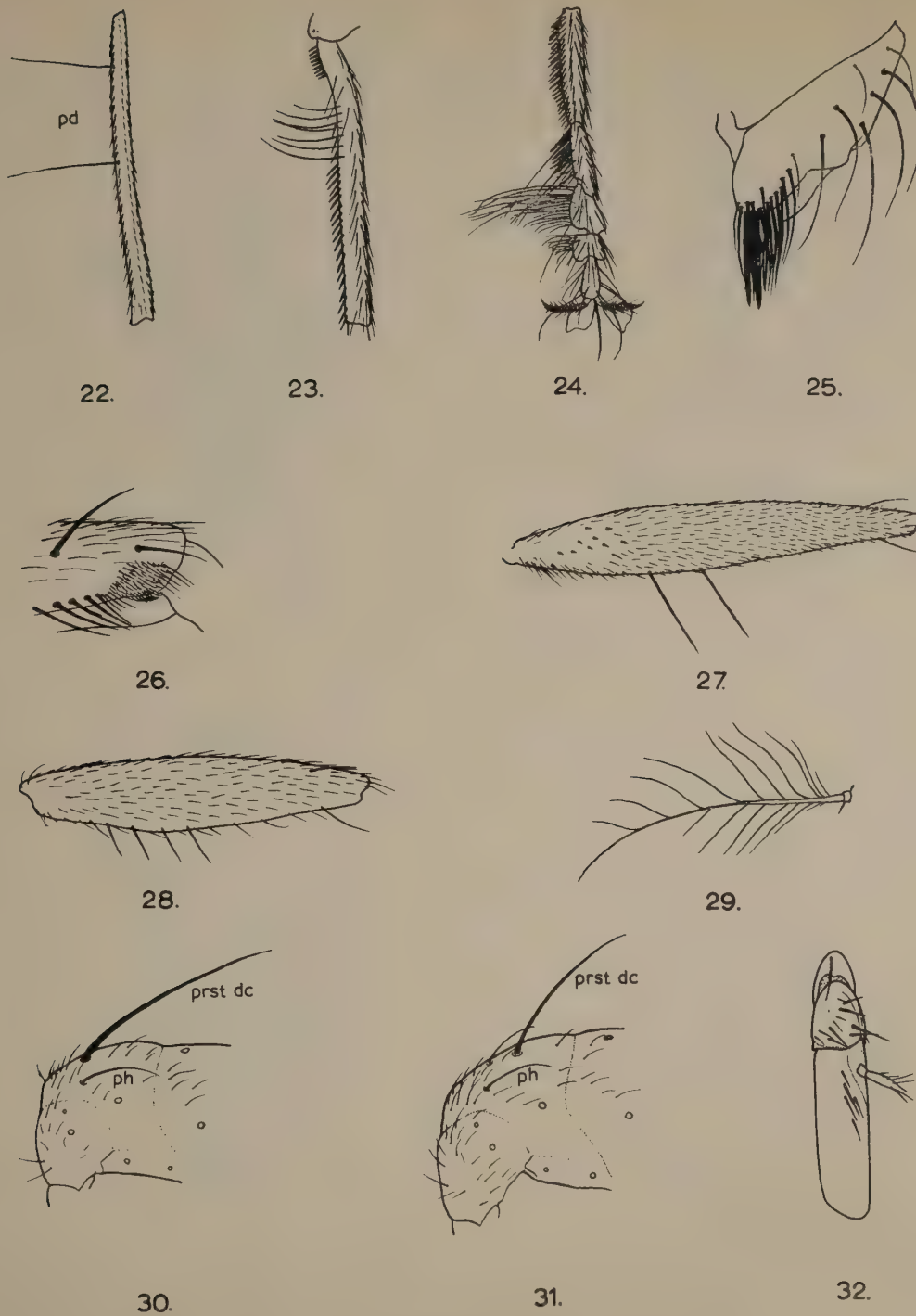
FIGURES 9-14

Fig. 9. ♂ mid femur of *P. respondens* (Walker), anterior view. Fig. 10. ♂ mid femur of *P. macularis* (Wiedemann), anterior view. Fig. 11. ♂ mid femur of *P. hirtimana* Malloch, posterior view. Fig. 12. ♂ mid femur of *P. acromiata* (Speiser), posterior view. Fig. 13. ♂ hind tibia showing preapical lobe in *P. intermedia* sp. n., anterior view. Fig. 14. ♂ hind tibia showing preapical lobe in *P. apicalis* Schiner, posterior view.



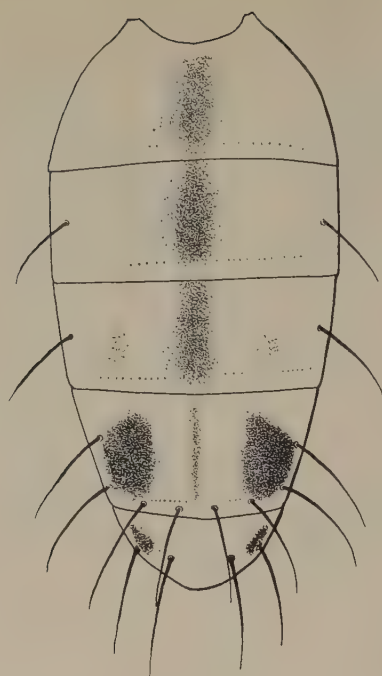
FIGURES 15-21

Fig. 15. ♂ hind tibia of *P. hirtimana* Malloch, anterior view. Fig. 16. ♂ hind tibia of *P. buxtoni* Malloch, dorsal view. Fig. 17. ♂ hind tibia of *P. absentiseta* sp. n., posterior view. Fig. 18. ♂ hind tibia of *P. lepidofera* (Stein), postero-dorsal view. Fig. 19. ♂ hind tibia of *P. simplex* Hennig dorsal view (♂ and ♀ similar). Fig. 20. ♂ mid tibia of *P. hirtimana* Malloch, showing sub-basal ventral notch. Fig. 21. ♂ mid tibia of *P. luteicornis* (Walker), posterior, view showing series of *pv* setae.

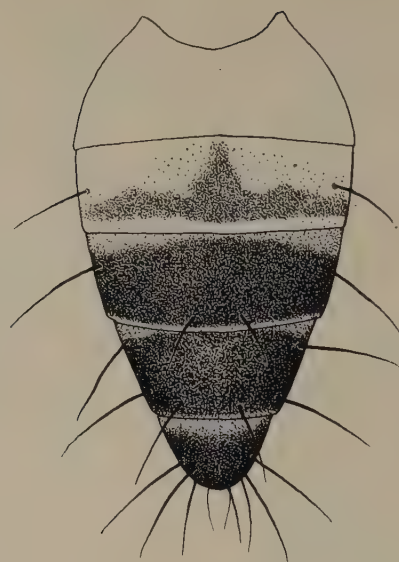


FIGURES 22-32

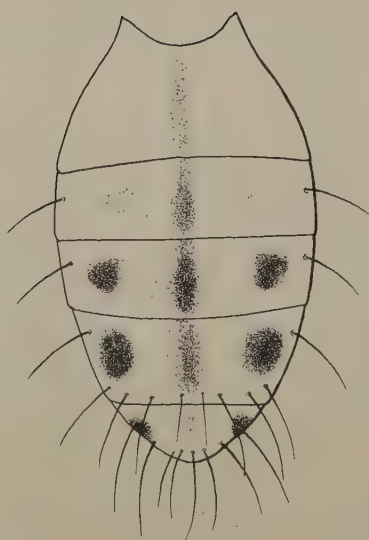
Fig. 22. ♂ mid tibia of *P. buxtoni* Malloch. Fig. 23. ♂ hind metatarsus of *P. setitarsis* Stein showing long *av* hairs. Fig. 24. ♂ hind tarsus of *P. hirtimana* Malloch. Fig. 25. Ventral view of ♂ mid coxa of *P. villicoxa* sp. n. Fig. 26. Apex of posterior surface of ♂ mid femur of *P. majalis* Paramonov. Fig. 27. Posterior view of ♂ hind femur of *P. buxtoni* Malloch. Fig. 28. Posterior view of ♂ hind femur of *P. liturata* (Walker). Fig. 29. Arista of *P. longipila* (Stein). Fig. 30. Prescutum of *P. alemella* Séguy. Fig. 31. Prescutum of *P. africana* sp. n. Fig. 32. Antenna showing setae on third segment in *P. seticornis* sp. n.



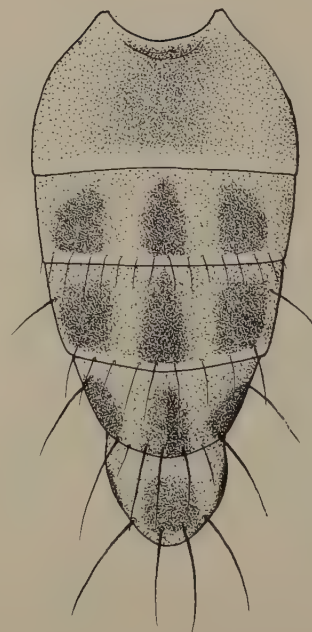
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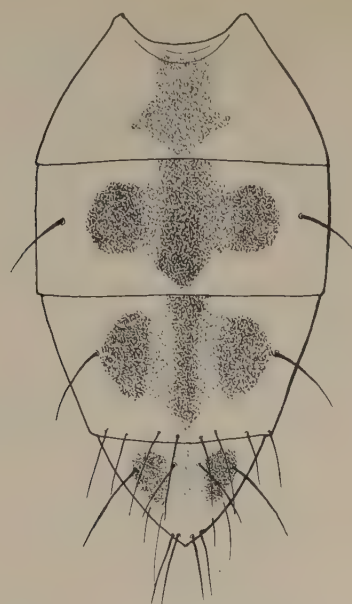
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FIGURES 33-36

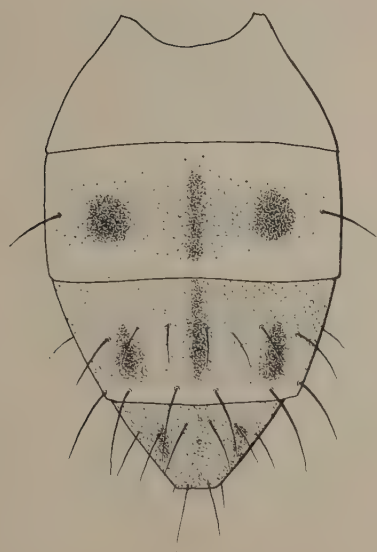
Fig. 33. Dorsal view of ♂ abdomen of *P. vittigera* sp. n. Fig. 34. Dorsal view of ♂ abdomen of *P. argentea* Paramonov. Fig. 35. Dorsal view of ♂ abdomen of *P. pallens* (Stein). Fig. 36. Dorsal view of ♂ abdomen of *P. keiseri* sp. n.



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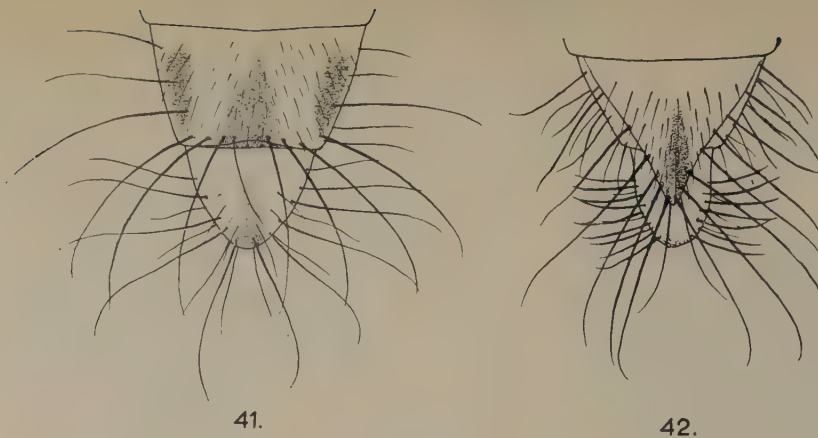
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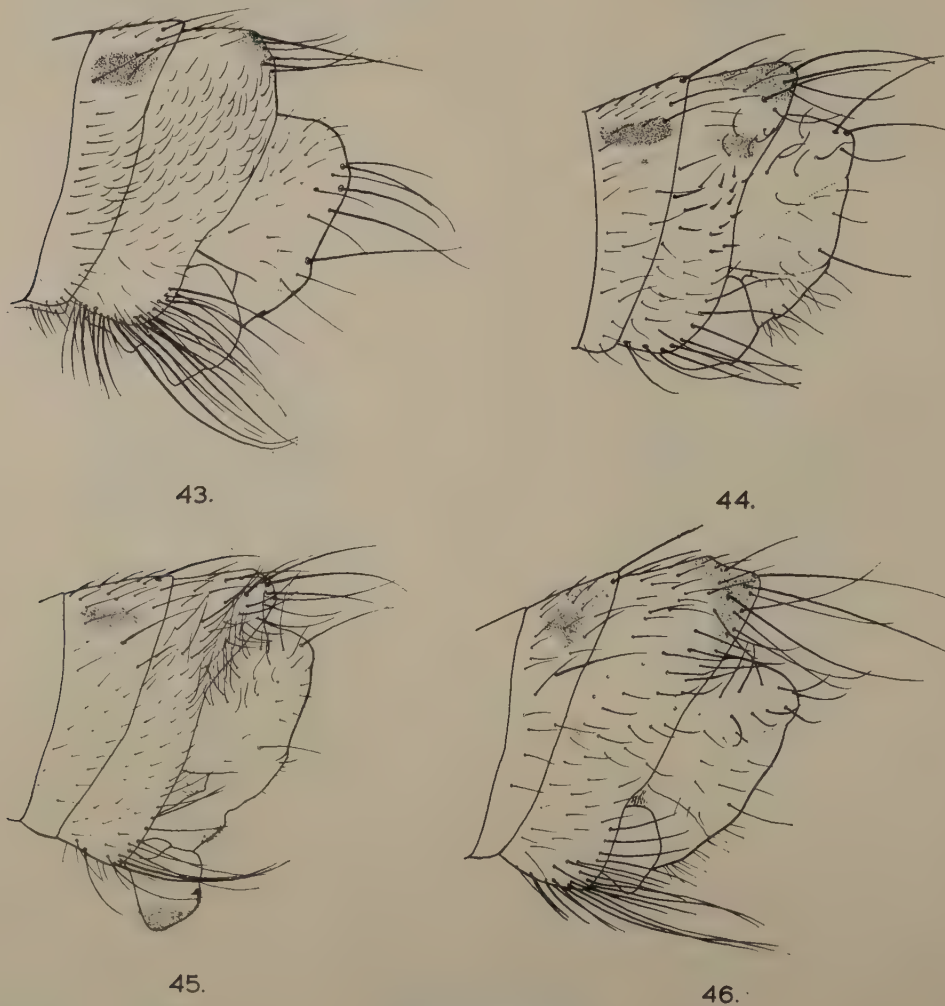
FIGURES 37-40

Fig. 37. Dorsal view of ♀ abdomen of *P. bakeri* sp. n. Fig. 38. Dorsal view of ♀ abdomen of *P. nigromaculata* sp. n. Fig. 39. Dorsal view of ♀ abdomen of *P. simplex* Hennig, showing transverse row of discal setae on T4. Fig. 40. Ventral view of apex of ♂ abdomen of holotype, *P. cheesmanae* sp. n.



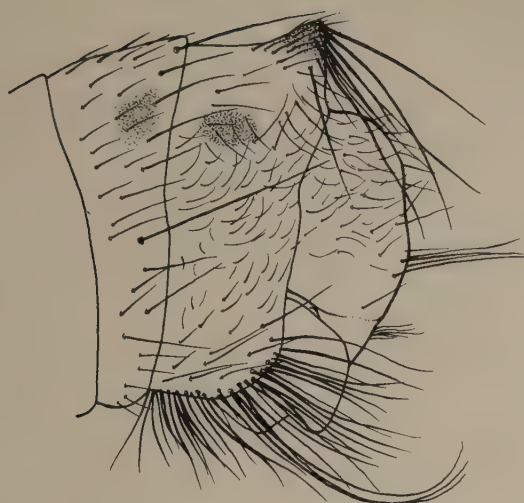
FIGURES 41 AND 42

Fig. 41. Dorsal view of apex of ♂ abdomen of *P. intermedia* sp. n. Fig. 42. Dorsal view of apex of ♂ abdomen of *P. maculipennis* Stein.

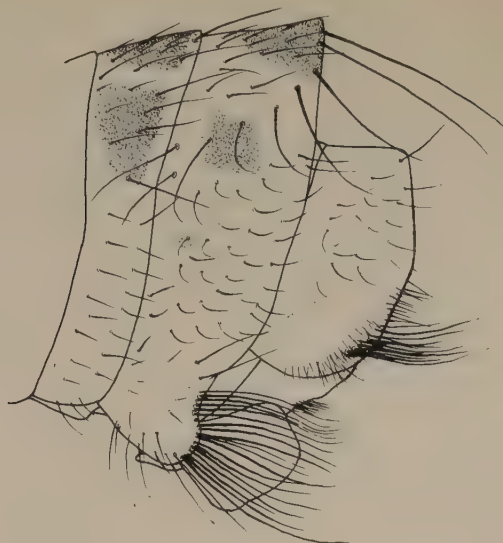


FIGURES 43-46

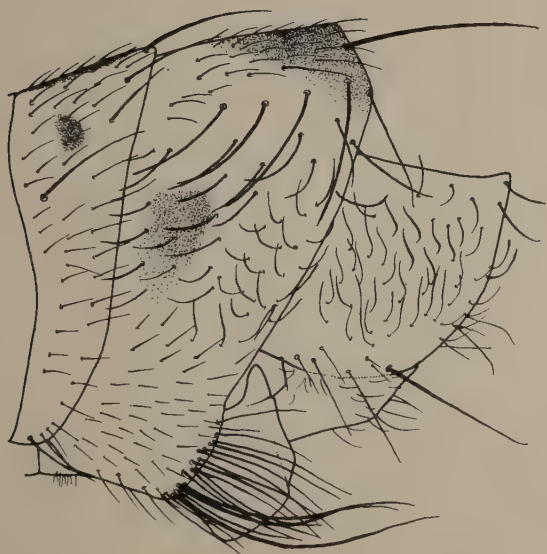
Fig. 43. Lateral view of apex of ♂ abdomen of *P. apicalis* Schiner. Fig. 44. Lateral view of apex of ♂ abdomen of *P. confusa* Stein. Fig. 45. Lateral view of apex of ♂ abdomen of *P. respondens* (Walker). Fig. 46. Lateral view of apex of ♂ abdomen of *P. macularis* (Wiedemann).



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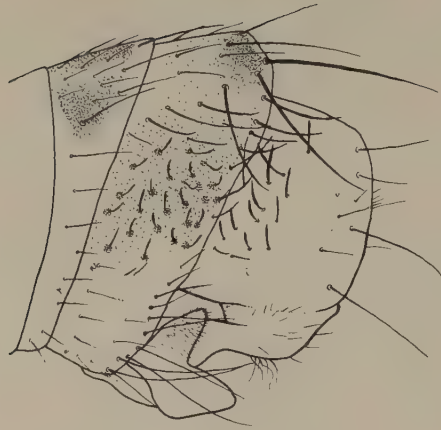
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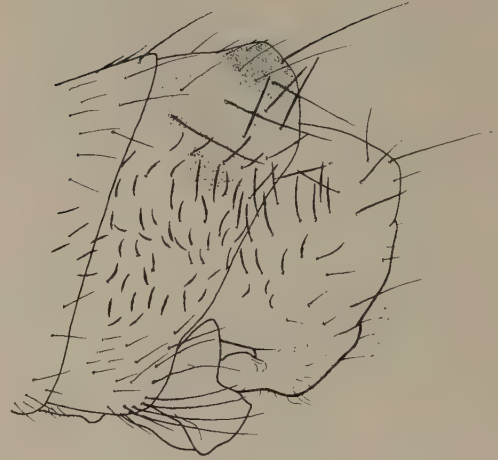
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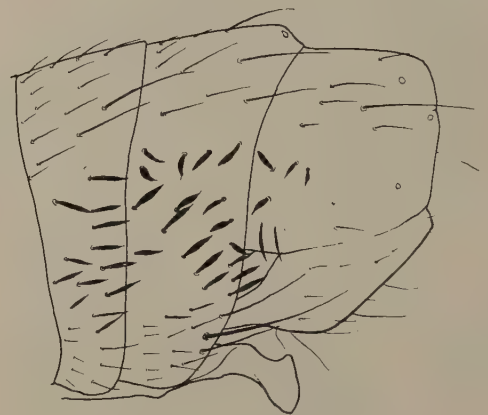
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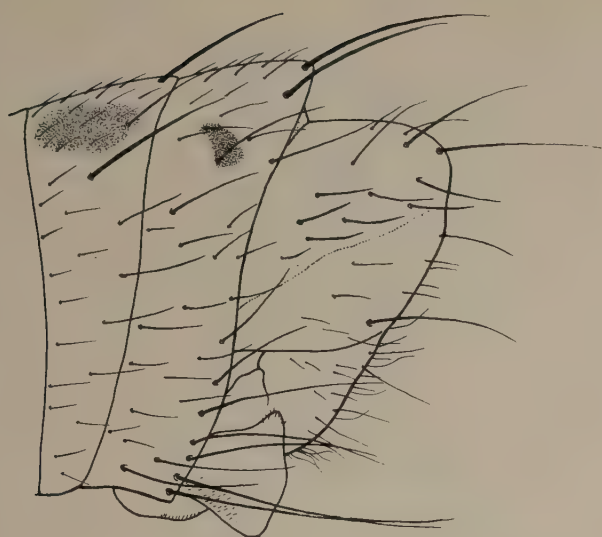
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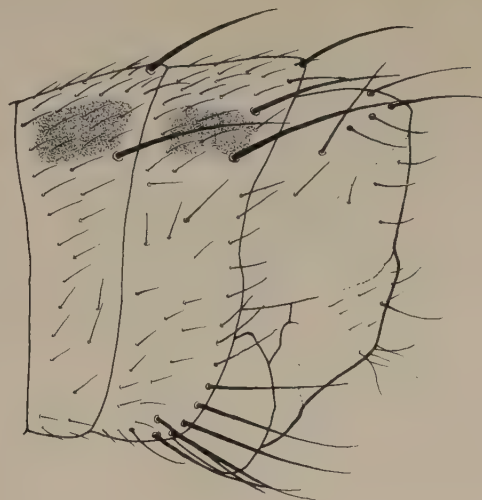
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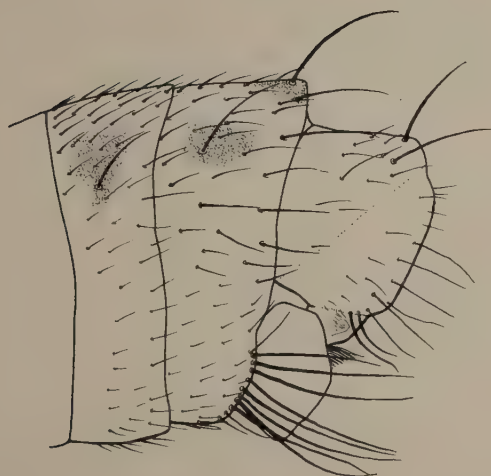
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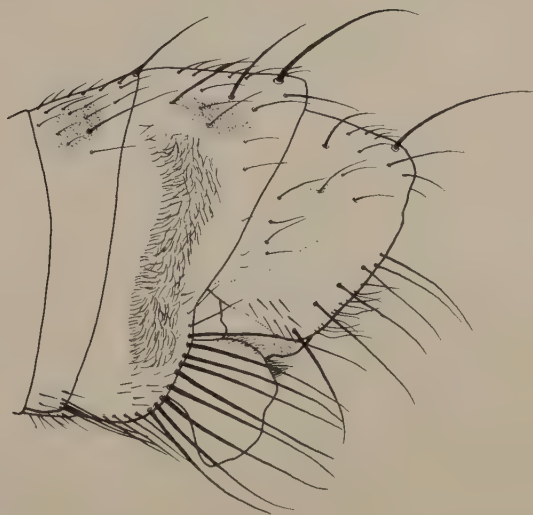
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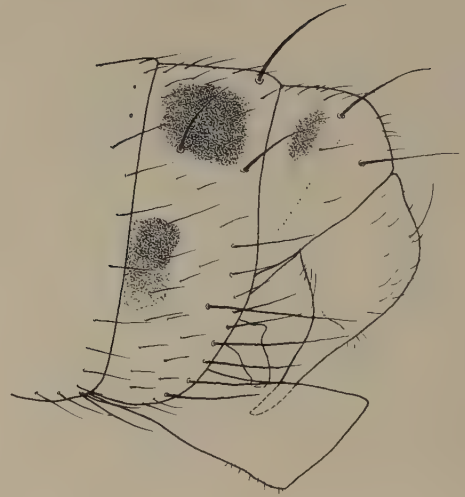
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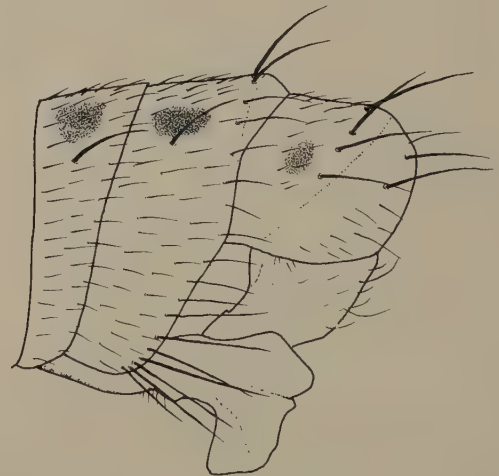
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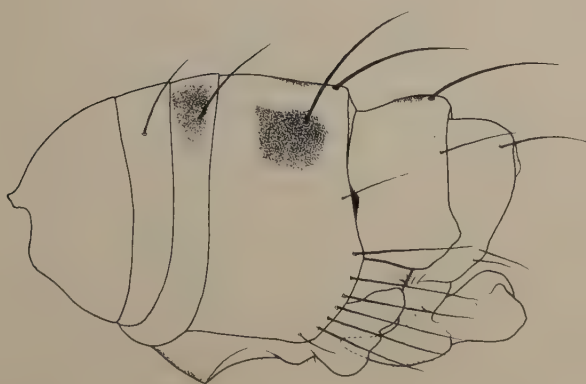
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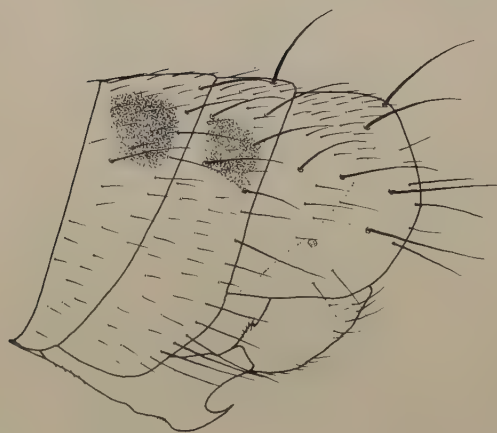
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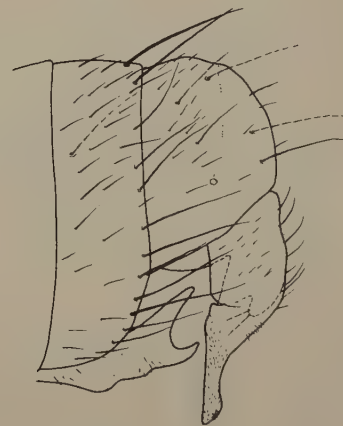
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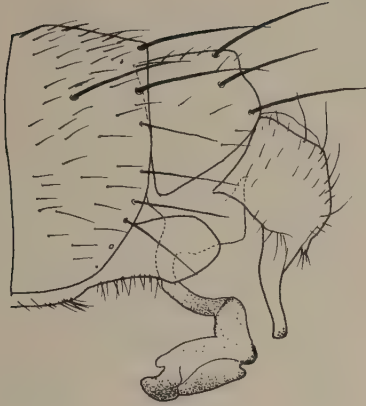
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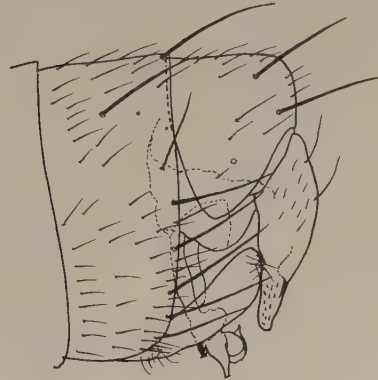
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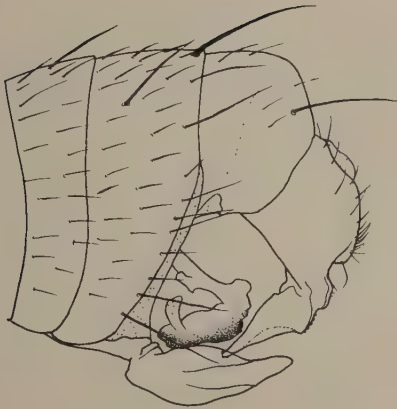
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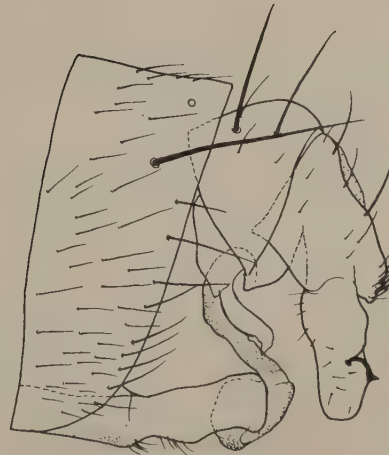
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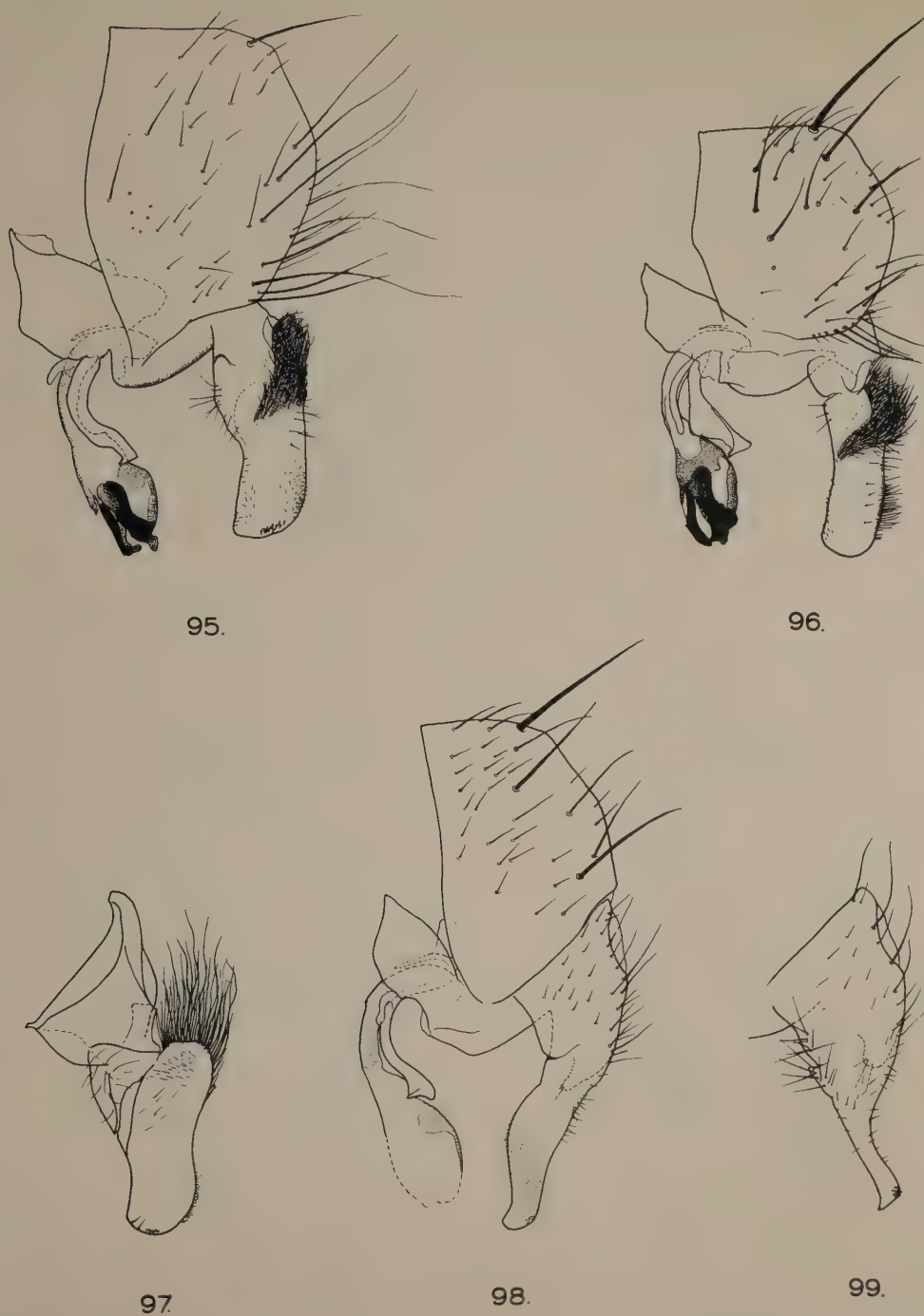
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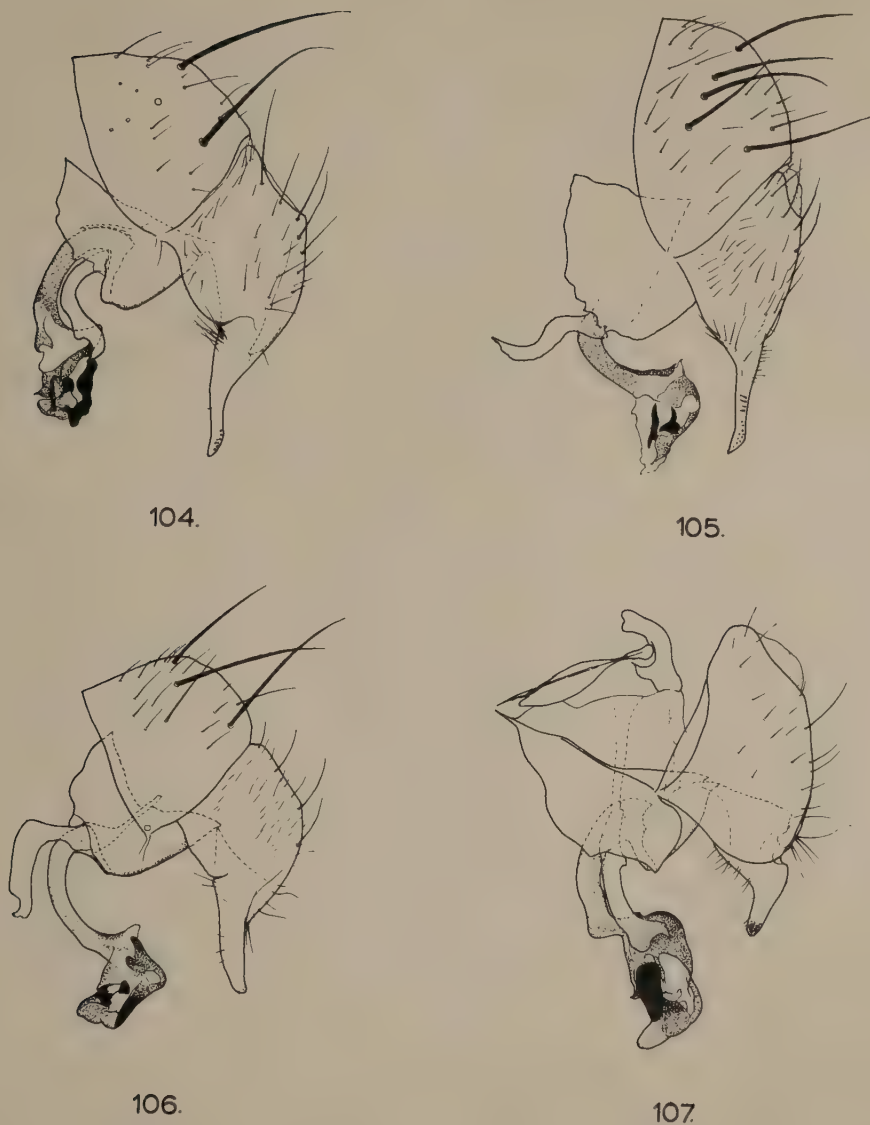
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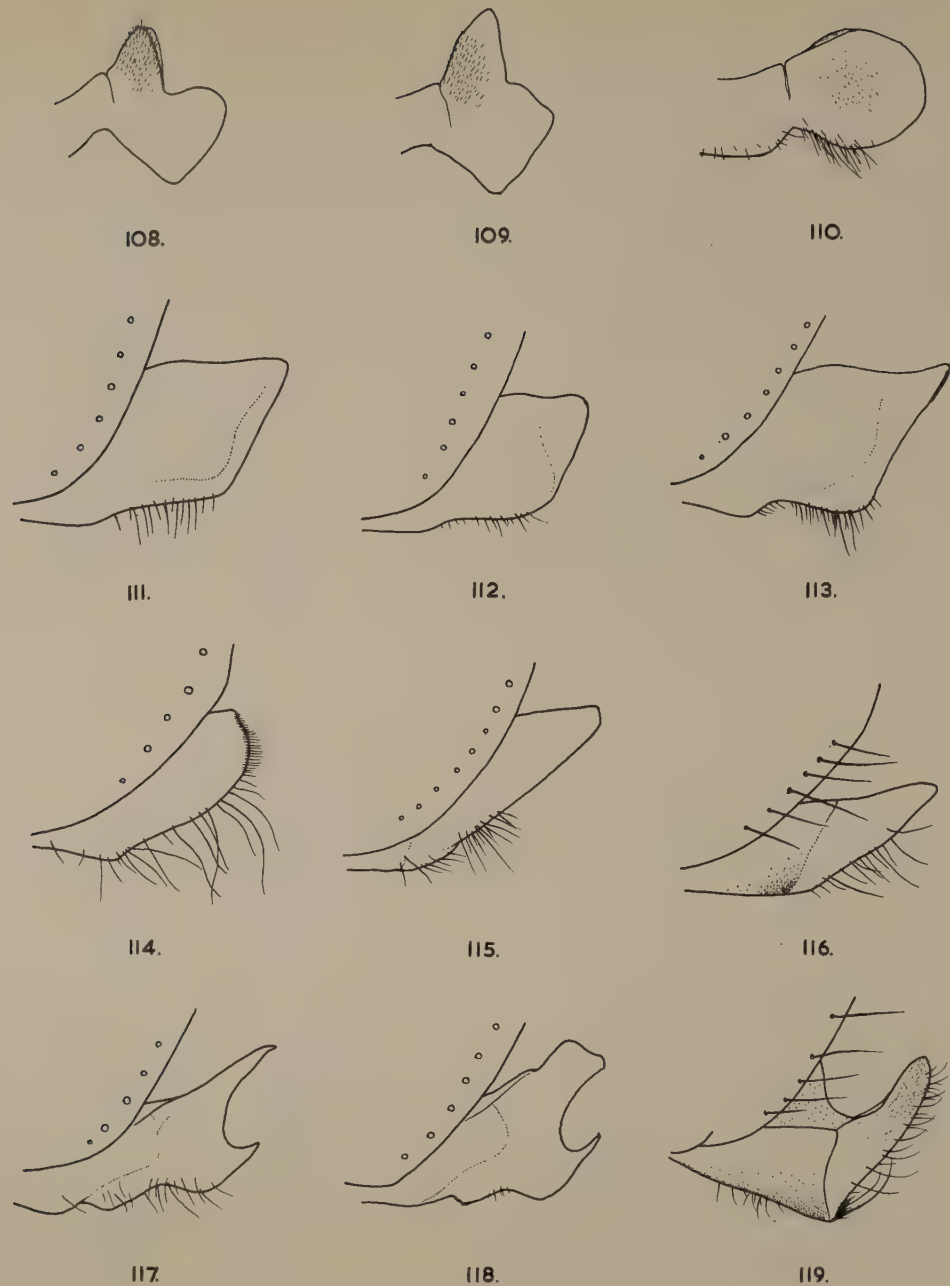
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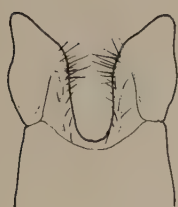
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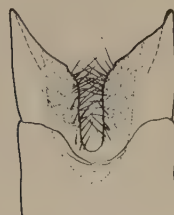


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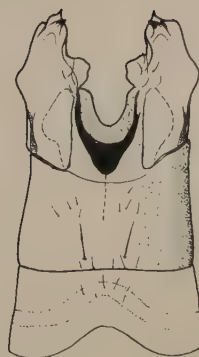
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The musculature of the primate shoulder

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(With 10 plates and 4 figures in the text)

SYNOPSIS

Several quantitative features of the shoulder muscles of monkeys and apes vary in such a way that an efficient mechanism is provided either for the type of quadrupedal locomotion found in many monkeys of both the Ceboidea (e.g. *Saimiri*) and Cercopithecoidea (e.g. *Papio*, *Cercopithecus*), for the brachiation characteristic of apes (e.g. *Hylobates*, *Pan*), or for a pattern of locomotion comprising a combination of each. This last is practised by certain species of monkeys ("semibrachiators") from both the New World (e.g. *Ateles*, *Lagothrix*) and the Old World (e.g. *Colobus*, *Rhinopithecus*).

Of the muscles contributing to the propulsive movement, *m. latissimus dorsi* is more powerfully developed and more cranially directed in brachiators than in quadrupeds and the pectoral musculature while directed laterally in the former, is orientated in a mainly cranial direction in the latter. Thus, as in the power stroke of locomotion, the forelimb can be most efficiently retracted from a raised position in brachiators and from a low position in quadrupeds.

The muscles responsible for raising the forelimb (*m. deltoideus*, *m. trapezius* and the caudal part of *m. serratus magnus*) are more powerfully developed in brachiators where the forelimb is relatively bigger and is raised above the head more frequently and for longer periods than in quadrupeds.

The strong development of the ventral edge of *m. latissimus dorsi*, of the caudal digitations of *m. serratus magnus* and of *m. deltoideus* provide, in brachiators, a mechanism for transmitting the weight of the trunk to the arm during suspension.

In semibrachiators, most features of the arm-raising and propulsive muscles are intermediate between those of quadrupeds and brachiators. They thus provide a mechanical compromise between systems specifically adapted for either method of progression.

In man, some features of the shoulder muscles (e.g. the transversely orientated pectoral mass and the powerful *m. deltoideus*) are like those of brachiators, while others (e.g. the size and disposition of both *m. latissimus dorsi* and the caudal part of *m. serratus anterior*) correspond with those of quadrupeds. The resulting arrangement may contribute to an overall mobility of the shoulder, more balanced than in monkeys and apes.

The contrasts in muscular features between those Prosimii that move quadrupedally (e.g. *Lemur*) and those which frequently hang from their extremities (e.g. *Perodicticus*) parallel those between quadrupeds and brachiators of the Anthropoidea. The most striking similarities affect the muscular features associated with transmitting the body weight to the arm, and can be related to the fact that, in both brachiators and prosimian "hangers," the forelimb is subject to predominantly tensile forces.

In addition to such major adaptive differences in the shoulder muscles, a number of meristic variations of no obvious mechanical significance contrast between equivalent taxonomic groups.

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INTRODUCTION

The muscular architecture of the primate shoulder as described in many scattered publications conforms to a basic pattern throughout the Order. Within this pattern, component muscles can be grouped either according to their topographical arrangement (e.g. Miller 1932) or to their presumed homologies (e.g. Howell 1936). But from a functional point of view derived from accounts of muscular disposition and attachments and from electromyographic studies (e.g. Inman, Saunders and Abbott 1944 ; Scheving and Paully 1959), the shoulder muscles comprise four distinct but interrelated groups.

Group 1 contains muscles that pass from the trunk to the humerus and retract the forelimb. In subhuman primates, where the forelimb plays a part in locomotion, these muscles contribute to the propulsive stroke. They consist firstly of *m. pectoralis major*, *m. pectoralis minor* and (in forms other than the Hominoidea) *m. pectoralis abdominalis*—these together forming the pectoral mass; and secondly, of *m. latissimus dorsi* with which *m. teres major* is closely associated.

Group 2 includes units that raise the forelimb. This movement comprises a lifting of the humerus by *m. deltoideus*, together with a rotation of the scapula by the cranial fibres of *m. trapezius* coupled with the caudal digitations of *m. serratus magnus*.

Group 3 comprises muscles extending from the scapula to the proximal part of the humerus, and which although having individual effects on movements of the arm, are collectively responsible for stabilizing the shoulder joint. This group contains *m. supraspinatus*, *m. infraspinatus*, *m. teres minor* and *m. subscapularis*.

Group 4 contains muscles that stabilize the shoulder girdle. It consists firstly of muscles inserted into the medial border of the scapula including (a) the cervical parts of *m. serratus magnus*—these, in the Hominoidea, forming a separate muscle : *m. levator scapulae*, (b) the parallel thoracic digitations of *m. serratus magnus* (or, in the Hominoidea, of *m. serratus anterior*) and (c) *mm. rhomboidei* ; secondly, two small muscles—*m. omohyoideus* and *m. subclavius* attached to the superior scapular border and to the clavicle respectively.

Within this plan occur certain variations of apparently little functional significance, but which nevertheless may be of taxonomic interest. For instance, Old World monkeys contrast with New World species in having the insertion of *m. teres major* typically fused with that of *m. latissimus dorsi* (Miller 1932).

But other qualitative differences, such as have emerged from restricted comparative studies by Miller (1932) and Campbell (1937), can be associated with functional contrasts—e.g. with variations in the method of locomotion. Thus, for instance, fibres attached to the tendon of *m. latissimus dorsi* and sweeping into the arm to form *m. dorsoepitrochlearis*, pass distally into the forearm in quadrupedal forms, and serve therefore to extend both the shoulder and elbow during the power stroke of quadrupedal locomotion. But in the apes, *m. dorsoepitrochlearis* inserts into the upper arm. Thus, as would appear to be advantageous in

brachiating, it assists adduction of the arm without impeding flexion of the elbow (cf. Wilder 1863).

The size and proportions of the shoulder muscles also appear to differ between locomotor groups. For instance, an analysis by Inman, Saunders and Abbott (1944) led to conclusions of the type that in man and the apes, *m. deltoideus* contributes a greater proportion to the total "scapulo-humeral" musculature (*m. supraspinatus*, *m. infraspinatus*, *m. teres minor*, *m. subscapularis*, *m. deltoideus* and *m. teres major*) than in monkeys. Again, *m. latissimus dorsi* and *m. teres major* are "most massive and extensive in climbing forms".

While accounts of individual species provide some basis for a more rigorous examination of qualitative variations in the shoulder muscles, the published data relating to muscular size and proportions are inadequate for this purpose, being restricted to the weights of individual muscles from some forty human subjects (Theile 1884), and from isolated subhuman primates (e.g. Haughton 1864, 1865).

TABLE 1
Locomotor and taxonomic subdivisions of the Anthroipoidea.

Locomotor group	Taxonomic group		
	Ceboidea	Cercopithecoidea	Hominoidea
Quadrupeds ..	<i>Aotes</i> , <i>Callicebus</i> , <i>Cacajao</i> , <i>Pithecia</i> , <i>Chiropotes</i> , <i>Cebus</i> , <i>Saimiri</i> , <i>Callimico</i> , <i>Callithrix</i> , <i>Leontocebus</i> .	<i>Macaca</i> , <i>Cynopithecus</i> , <i>Cercocebus</i> , <i>Papio</i> , <i>Comopithecus</i> , <i>Mandrillus</i> , <i>Theropithecus</i> , <i>Cercopithecus</i> , <i>Allenopithecus</i> , <i>Erythrocebus</i> .	
Semibrachiators	<i>Alouatta</i> , <i>Ateles</i> , <i>Brachyteles</i> , <i>Lagothrix</i> .	<i>Presbytis</i> ,* <i>Rhinopithecus</i> , <i>Nasalis</i> , <i>Colobus</i> .	
Brachiators ..			<i>Hylobates</i> , <i>Symphalangus</i> , <i>Pongo</i> , <i>Pan</i> , <i>Gorilla</i> .

Insufficient information is available to classify the genera *Pygathrix* and *Simias*.

* The genus *Presbytis* contains many species which are true semibrachiators. The species: *entellus*, *priamus*, *schistaceus*, *hypolucaeus*, appear to be semibrachiators when in the trees. But they also spend considerable amounts of time on the ground where they move quadrupedally.

The deficiencies of the published anatomical data are further accentuated when viewed in relation to the studies of Erikson (1954), Napier (1959) and Napier and Davis (1959). These elaborate the thesis, foreshadowed by Campbell (1937), that in addition to the brachiation practised by all apes when in the trees and the quadrupedal progression of many monkeys both in the trees (e.g. *Saimiri*, *Cercopithecus*) and on the ground (e.g. *Papio*), there is found in certain monkeys a method of locomotion described as "semibrachiation" (Napier 1961). In this "the arms lead the way, reaching in front of or above the head to grasp at hand holds, or to grab at branches when jumping from tree to tree" (Napier 1959).

Napier mentions a number of groups (e.g. *Lagothrix*, *Colobus*) which adopt this type of locomotion, and more recently, the list has been extended by a systematic study of primate locomotion based on information scattered throughout the literature, and on data obtained from an examination of living animals and of films recording their movements (Ashton and Oxnard 1963). This study has verified that in semibrachiators the use of the arms for suspension, although more restricted than in apes, is more extensive than in quadrupedal monkeys. There is considerable variation within this group, the locomotor pattern characteristic of *Ateles*, for instance, being more like that of brachiators, while that of *Colobus* inclines towards the pattern found in quadrupeds. Semibrachiators appear to be restricted to certain taxonomic subdivisions of both the Ceboidea and Cercopithecoidea (Table 1).

Differences in locomotor patterns among the Prosimii parallel, in some respects, variations seen in the Anthropoidea. Thus, *Lemur* and *Tupaia* are fully quadrupedal, while other species (e.g. *Galago*) sometimes move quadrupedally but at others progress by long leaps, landing on all four extremities simultaneously.

TABLE 2
Locomotor and taxonomic subdivisions of the Prosimii.

Locomotor group	Taxonomic group		
	Lemuriformes	Lorisiformes	Tarsiiformes
Quadrupeds ..	<i>Tupaia</i> , <i>Anathana</i> , <i>Dendrogale</i> , <i>Tana</i> , <i>Urogale</i> , <i>Ptilocercus</i> , <i>Hapalemur</i> , <i>Lemur</i> , <i>Lepilemur</i> , <i>Cheirogaleus</i> , <i>Microcebus</i> , <i>Phaner</i> , <i>Daubentonia</i> .	<i>Galago</i> , * <i>Euoticus</i> *.	<i>Tarsius</i> *.
Hangers ..	<i>Lichanotus</i> , <i>Indri</i> , <i>Propithecus</i> .	<i>Loris</i> , <i>Nycticebus</i> , <i>Arctocebus</i> , <i>Perodicticus</i>	

* Hoppers.

In other groups (e.g. *Perodicticus*, *Loris*, *Nycticebus*), although the animal sometimes moves quadrupedally, it often suspends itself by all four extremities and progresses while inverted. Yet other species (e.g. *Indri*, *Propithecus*) habitually leap from tree to tree and land in a vertical position, holding on to branches with the forelimb. With respect to the function of the forelimb these two latter groups of species can be collectively designated "hangers".

The distribution of the various genera within these locomotor groups is outlined in Table 2.

The present study has been undertaken firstly, to augment the existing qualitative information about variation in the shoulder musculature of different primate species; secondly, to provide corresponding quantitative information about relative muscular proportions; thirdly, to enquire whether or not the detailed findings can be functionally related to variations in the method of locomotion adopted by different primate groups.

MATERIALS AND METHODS

Material

The study was based on fifty-three dissections representing six genera from the Prosimii and twenty-three from the Anthropoidea. Some specimens were from the collection in the Department of Anatomy, University of Birmingham, others were from the private collections of Professor Sir Solly Zuckerman, Professor A. J. E. Cave and Dr. W. C. Osman Hill. Further material was provided by the Zoological Society of London.

Specimens ranged in age from the stage following the eruption of the complete milk dentition to maturity.

The material had been fixed in formalin and had been stored for a variable period either in a solution of formal saline or in a mixture of propylene phenoxetol and glycerine.

Grouping of material

In the Anthropoidea, sufficient material was available to enable a complete subdivision to be effected into the locomotor groups: quadrupeds, semibrachiators and brachiators, together with man. As relatively few Prosimii were available, it was practicable to divide into two groups only. Group 1 contained those types in which the arm is subject almost exclusively to forces of compression, irrespective of whether the animal moves quadrupedally (e.g. *Tupaia*, *Lemur*), or by hopping (e.g. *Galago*). In subsequent descriptions, this combined group is referred to as "quadrupeds". Group 2 comprised those types which, to a great or lesser extent, suspend themselves from the forelimb (e.g. *Propithecus*, *Loris*, *Nycticebus*, *Perodicticus*) and which, in subsequent descriptions are, as already noted, designated "hangers".

Distribution of the available material between locomotor groups is outlined in Table 3.

*Qualitative study**Dissection*

The superficial and deep muscular layers on the dorsal and ventral aspects of the specimens were exposed and photographed, careful examination being made of the form and disposition of the individual units.

Anatomical nomenclature

Wherever possible, use has been made of the descriptive terms applicable to human anatomy set out in the "Nomina Anatomica" (1955), the terminology of Howell and Straus (1933) being inserted in the remaining instances. But the formal Latin names have been used only for muscles, ligaments and fascial sheets, anglicized derivatives being applied to other structures.

In most subhuman forms, m. teres minor is morphologically inseparable from m. infraspinatus, but as these muscles have a different nerve supply and are, in many

non-primate mammals, as in man, morphologically distinct (Howell and Straus 1933), the composite mass is, in subsequent descriptions, referred to as mm. infraspinatus et teres minor.

TABLE 3
Division of the available material into locomotor groups.

Locomotor group	Species	Number dissected	Number weighed
Quadrupeds	<i>Aotes</i>	2	2
	<i>Callicebus</i>	1	1
	<i>Cacajao</i>	1	1
	<i>Pithecia</i>	2	2
	<i>Saimiri</i>	1	1
	<i>Callithrix</i>	5*	4*
	<i>Leontocebus</i>	2*	1*
	<i>Macaca</i>	5*	4*
	<i>Cercocebus</i>	1*	0*
	<i>Papio</i>	1	1
	<i>Comopithecus</i>	1	1
	<i>Mandrillus</i>	1	1
	<i>Cercopithecus</i>	5*	4*
Semibrachiators	<i>Alouatta</i>	1	1
	<i>Lagothrix</i>	1	1
	<i>Ateles</i>	1	1
	<i>Colobus</i>	2	2
Brachiators	<i>Hylobates</i>	2	2
	<i>Symphalangus</i>	1	1
	<i>Pongo</i>	1	1
	<i>Pan</i>	2	2
	<i>Homo sapiens</i>	3	3
Prosimian quadrupeds ..	<i>Tupaia</i>	1	1
	<i>Lemur</i>	1	1
	<i>Galago</i>	4*	3*
Prosimian hangers ..	<i>Propithecus</i>	1	1
	<i>Nycticebus</i>	2	2
	<i>Perodicticus</i>	1	1

* Single specimens of *Callithrix*, *Leontocebus*, *Macaca*, *Cercocebus*, *Cercopithecus* and *Galago* were dissected but could not be weighed.

For the purpose of functional analysis it appeared appropriate to separate the fibres of m. serratus magnus (or, in the Hominoidea, of m. levator scapulae plus m. serratus anterior) that insert into the vertebral border of the scapula above the inferior angle and whose main function appears to be to stabilize the scapula, from the fan-like digitations of this muscle that insert near the inferior angle and which help to rotate the bone. In subsequent descriptions of prosimians and monkeys, the former are referred to as m. serratus magnus pars cranialis and the latter as m. serratus magnus pars caudalis. In descriptions of apes and man, they are listed

respectively as *m. levator scapulae* plus *m. serratus anterior pars cranialis* and as *m. serratus anterior pars caudalis*.

Pattern of description

Descriptions of the shoulder musculature in the Anthroidea and in the Prosimii are presented separately. Within each of these taxonomic divisions, accounts are given of individual muscles firstly of the group primarily responsible for propulsion, secondly of those responsible for raising the arm, thirdly of the stabilizers of the shoulder joint, and fourthly of the fixers of the scapula.

For each muscle, a description is first given of the features common to all locomotor groups within the appropriate suborder.

Next are enumerated the principal features that vary markedly between the different locomotor groups. The accounts given (which, to maintain a uniform pattern of description, include those for man) are based entirely on the specimens dissected in the present study. The published accounts, limited in many instances to descriptions of single species, fail to accentuate many of the points of contrast between locomotor groups that emerged from the present comparative study, but such relevant general information as they convey (e.g. about the relative development of different groups of fibres) supports the new observations.

Finally, detailed accounts are given of variation between the individual representatives of each locomotor group. Attention is also drawn, firstly to the other variations relating to these species that have been reported in the literature, and secondly to variations from the general pattern that have been described for species that were not available for study. In the case of man, attention is drawn only to the more salient published studies.

In the text, there are brief tabular summaries of the segmental extent of various muscles—the information being derived from the new data compounded with that published in the literature.

Statistical study

Muscle weights

Following its dissection, each muscle was detached and immersed in preservative for a week in order to ensure, so far as possible, an even permeation of fluid. Superficial moisture was then removed and the muscle weighed. The quantitative data obtained from our study of three human subjects were supplemented by figures derived from eighteen adult individuals of recorded sex (Theile 1884). Theile does not give separate weights for the cranial and caudal parts of *m. serratus anterior*, and to make his data comparable with our own, the weight of *m. serratus anterior* was, in each individual, divided according to the average value of the ratio between the weights of the cranial and caudal parts of this muscle in our three human subjects.

Precision of weighing

The weights of individual muscles were recorded to the nearest 0.5 per cent. As a check on the accuracy of the procedure, muscles of four specimens of the

rhesus monkey (*Macaca mulatta*) were each weighed six times at weekly intervals, the muscles being stored in preservative during the intervening periods. Analyses of the resulting data showed that, in all cases, the variance introduced artificially as a result of fluctuations in the recorded weight was quite insignificant ($P > 0.2$) compared with that existing between animals. It is therefore unlikely that errors due to inaccuracy in weighing and to differences in the degree of hydration of different muscles could have materially affected the final result.

Proportionate muscle weights

In order to reduce any bias in the results of quantitative comparisons consequent upon differences in gross size or in the degree of fixation of individual specimens, study was restricted to an analysis of the ratios listed in Tables 13 and 23. In many of these, the weight of the muscular mass comprising the stabilizers of the shoulder joint together with the fixers of the scapula was used as the denominator because morphological study had shown them to be relatively constant in form and disposition throughout the primates.

Sex and age differences in proportionate weights

Insufficient specimens of any subhuman primate were available to permit an examination of sexual differences in the composition of the shoulder musculature. But comparisons based on the data from eleven adult men and seven adult women (Theile 1884) showed that except in the case of the pectoral muscles which were significantly bigger ($P < 0.02$) in males, proportionate composition of the shoulder musculature was similar in the two sexes. If, therefore, the results derived from an analysis of data relating to man can be applied to other primate groups, it is unlikely that the overall picture of contrast is appreciably distorted by pooling data derived from individuals of different sex.

Theile's monograph also included data for ten immature individuals whose ages ranged from late foetal life to adolescence. Analysis of these figures indicated that while certain significant differences in the proportionate composition of the shoulder musculature may occur in early postnatal life, adult proportions are practically attained by the time the complete milk dentition has erupted—i.e. at the age of the youngest specimen of any species dissected in the present study.

Grouping of material and computation of basic statistical data

Preliminary analysis confirmed that differences between (a) arboreal quadrupeds (Cercopithecoidea), (b) terrestrial quadrupeds (Cercopithecoidea), (c) arboreal quadrupeds (Ceboidea—Callithricidae) and (d) arboreal quadrupeds (Ceboidea—Cebidae), were both small in size and readily attributable to chance ($P > 0.05$). Basic data were accordingly computed for all quadrupedal monkeys. Data relating to (a) brachiators and (b) semibrachiators were also tabulated and the mean and standard error computed for each proportionate weight or ratio.

Basic statistical data for man were computed from the combined figures derived from the muscle weights of the three specimens dissected in the present study and from the data recorded by Theile (1884).

For the Prosimii, corresponding basic data were computed for (a) quadrupeds and (b) hangers.

Precision of basic data

As judged by the ratio of the standard error of the mean to the mean itself, the data proved less precise than is usual in anthropometric studies. Thus, in the Anthropoidea, the standard error of the mean was less than five per cent of the mean itself in thirty-three of the forty-eight indices (twelve in each of four locomotor groups). In the remaining fifteen cases, the standard error lay between five and ten per cent of the mean. But in the Prosimii, where relatively few specimens were available, the standard error was greater than ten per cent. of the mean in eleven of the twenty-four indices (twelve in each of two locomotor groups). Nevertheless, the estimates were, in each suborder, adequate to establish many differences between locomotor groups, as significant statistically.

Comparison between locomotor groups

For the Anthropoidea, the significance of differences in the mean value of each measurement or index in (a) quadrupeds (b) semibrachiators (c) brachiators and (d) man was assessed by means of analyses of variance and *t* tests.

The significance of differences between corresponding mean values in the two groups of Prosimii [(a) quadrupeds and (b) hangers] was assessed by means of *t* tests.

Qualification of the results

In addition to the fact that even when specimens of both sexes and widely differing age were pooled, statistical estimates sometimes remained imprecise, the results of this study are subject to certain qualifications, viz :—

(1) A separation of the monkeys and apes into quadrupeds, semibrachiators and brachiators is, to some extent, artificial, a detailed analysis of locomotor patterns (Ashton and Oxnard 1963) having shown that there is an almost continuous range of variation extending from terrestrial quadrupeds (e.g. *Papio*) to extreme brachiators (e.g. *Hylobates*). Again, in the Prosimii, the hangers include types that contrast markedly in locomotor pattern.

(2) A division of the shoulder musculature into (a) propulsive muscles (b) arm-raising muscles (c) fixers of the shoulder joint and (d) fixers of the shoulder girdle is to some extent arbitrary : firstly because the precise function of individual muscles has not been determined by comparative electromyographic study, and secondly because certain muscles make a functional contribution to more than one subgroup.

(3) Although the consideration of the Prosimii as a separate group has enabled most of the smallest specimens of the series to be separated and compared with each other, certain locomotor groups of the Anthropoidea include species of widely differing body size. It is not known whether or not the proportionate composition of the shoulder musculature is influenced by the absolute size of different individuals.

RESULTS

Qualitative description of dissections

(ANTHROPOIDEA)

*Muscles responsible for propulsion**M. pectoralis major*

General description: *M. pectoralis major* is a prominent triangular muscle, lying superficially, taking a fleshy origin from the ventral surface of the thoracic cage, and inserting by means of a short tendon into the lateral lip of the intertubercular groove. Near the insertion, the more caudally-disposed fibres pass deep to the distal margin of the remaining part of the muscle, the caudal border thus being folded inwards upon itself. Consequently, the tendon comprises two laminae continuous at their distal border.

Principal contrasts between locomotor groups: (Pls. 1-7 and Table 4) : In quadrupeds, the origin of this muscle is relatively long and its caudal part is strongly developed. The direction of the fibres, while to some extent lateral, is predominantly cranial, and there is little infolding of the caudal margin.

In semibrachiators, the origin is shorter than in quadrupeds. The contrast in the development of the cranial and caudal parts of the muscle is less marked, the direction of the caudal fibres is more lateral and the tendon appears to be more folded.

In brachiators, the origin of *m. pectoralis major* is even shorter. The caudal part of the muscle is thinner than the cranial part, and the direction of the fibres in both regions is predominantly lateral. The tendon is more folded than in either quadrupeds or semibrachiators.

In man, these features are similar to those in brachiators.

Variation: (a) *quadrupeds:* (Pl. 1, fig. 1 and Pl. 2, fig. 5) : The muscle was incompletely divided by a fibrous raphe into two heads. The first (*pars sternoclavicularis*) arose from the capsule of the sternoclavicular joint and the manubrium. A similar origin was characteristic of most cases described in the literature, but Champneys (1872) described a specimen of *Cynocephalus* (= *Papio*) *anubis*, in which certain of the most cranial fibres arose from the medial end of the clavicle, while Dobson (1881) described a specimen of *Cercopithecus* in which the origin extended along "almost the whole length" of this bone.

The second head (*pars sternocostalis*) was always the bigger and arose from the sternbrae and from the costal cartilages of certain false ribs, the caudal limit being usually the eighth costal cartilage (Table 4). In our specimens of *Papio*, *Comopithecus* and *Mandrillus*, and in a specimen of *Cynopithecus* (Patterson 1942) some fibres of this head also took origin from the uppermost part of the aponeurosis of *m. obliquus externus abdominis*.

The caudal part of the *pars sternocostalis* was, in all quadrupeds, thicker than the cranial region.

The cranial part of *m. pectoralis major* was directed laterally, but fibres of the intermediate and caudal regions mainly passed cranially.

The more cranial fibres of the pars sternocostalis inserted with those of the pars sternoclavicularis into the superficial lamina of the tendon, and only the fibres of the strongly-developed caudal region of the pars sternocostalis gained attachment to the deep lamina.

(b) *semibrachiators*: (Pl. 3, fig. 9 and Pl. 4, fig. 13) : As in quadrupeds, m. pectoralis major always comprised two parts joined by a fibrous raphe, but the pars sternoclavicularis was the more prominent. Its fibres were attached not only to the manubrium and to the capsule of the sternoclavicular joint but extended both caudally on to the sternebrae (as far as the third sternocostal junction) and cranially on to the clavicle. In the available specimens of *Alouatta*, *Ateles* and *Lagothrix*, these fibres covered the medial half of the clavicle, but in those of *Colobus*, they extended for a short distance only over its medial end. In one of three specimens of *Lagothrix* described by Robertson (1944), the most cranial fibres extended over only its medial third. In the specimen of *Rhinopithecus* described by Patterson (1942) no fibres gained attachment to the clavicle.

In contrast to m. pectoralis major of quadrupeds, the pars sternocostalis was always uniformly thin, and its origin from the sternebrae usually extended only as far as the level of the fifth or sixth rib (Table 4).

As in quadrupeds, the pars sternoclavicularis passed almost directly laterally, but the direction of the pars sternocostalis was more lateral than in quadrupedal monkeys.

The pars sternoclavicularis was, as in quadrupeds, inserted superficially into the lateral lip of the intertubercular groove, but in contrast to quadrupedal monkeys almost all fibres of the pars sternocostalis were inserted deep to those of the pars sternoclavicularis.

In one of three specimens of *Lagothrix*, described by Robertson (1944), m. pectoralis major inserted into both lips of the intertubercular groove, the tendon splitting in its upper part to form an arch through which passed the tendon of the caput longum of m. biceps brachii.

(c) *brachiators*: (Pl. 5, fig. 17 and Pl. 6, fig. 21) : In this group, m. pectoralis major comprised : pars clavicularis, pars sternocostalis and pars abdominalis. In our specimens of *Hylobates*, *Symphalangus* and *Pan*, adjacent heads were connected by fibrous raphes. In the specimen of *Pongo* and in the descriptions of *Gorilla* published by Stewart (1936) (one specimen) and Raven (1950) (two specimens), adjoining parts were separated by triangular spaces filled with loose areolar tissue.

The pars clavicularis arose firstly from the clavicle [extending over its medial two thirds in *Hylobates* and *Symphalangus*, over its medial half in *Pan*, over its medial quarter in *Gorilla* (Stewart 1936 ; Raven 1950) and for only a short distance in *Pongo*] and secondly from the capsule of the sternoclavicular joint and manubrium.

The pars sternoclavicularis took origin from the body of the sternum and from a variable number of costal cartilages (usually the first to the fifth). The pars abdominalis generally took origin from costal cartilages 5, 6 and 7 and from the adjoining aponeurotic parts of m. obliquus externus abdominis. Variations in the caudal limit of origin are listed in Table 4.

The pars clavicularis and the pars sternocostalis were thicker than the pars abdominalis.

The fibres of the pars clavicularis passed laterally and somewhat caudally. Those of the pars sternocostalis were directed laterally while those of the pars abdominalis passed laterally and to some extent cranially.

The fibres of both the pars sternocostalis and the pars abdominalis were attached to the deep lamina of the tendon of insertion, those of the pars abdominalis lying proximal to those of the pars sternocostalis. In the available specimens of *Hylobates* and *Symphalangus*, part of the deep lamina of the tendon was fused with the tendon of origin of the caput longum of m. biceps brachii.

(d) *man*: (Pl. 7, fig. 25) : In two of our three subjects, m. pectoralis major consisted of a pars clavicularis and a pars sternocostalis separated by loose areolar tissue. Perrin (1871) and Bryce (1899) have each described separation of these heads by a big triangular gap.

In the three available subjects, the pars clavicularis arose from the medial half of the clavicle, the capsule of the sternoclavicular joint and the manubrium. Perrin (1871) and Bryce (1899) have described examples of the replacement of most of the pars clavicularis by white fibrous tissue, some few fleshy fibres taking origin from the manubrium. Perrin (1871) has also drawn attention to a separation of the pars clavicularis from the pars sternocostalis by a big triangular gap and its fusion with the anterior border of m. deltoideus.

The pars sternocostalis took origin, in each of the available subjects, from the sternum, the second to the seventh costal cartilages and the adjacent aponeurotic parts of m. obliquus externus abdominis.

In one subject, a muscular slip from the rectus sheath formed a pars abdominalis of m. pectoralis major. It was separated by loose areolar tissue from the inferior border of the pars sternocostalis. Perrin (1871) found a corresponding slip in eleven (nineteen per cent) of a series of fifty-eight human subjects, and Loth (1932, cit. Matsuo 1960) has reported its occurrence in sixty-five per cent of individuals.

Perrin (1871), Bryce (1899) and Landry (1958) have described a total of five instances in which a muscular slip (m. chondroepitrochlearis) was present. This arose immediately distal to the inferior border of the pars sternocostalis, passed supero-laterally towards the main insertion and then distally in the groove between m. biceps brachii and m. coracobrachialis, to insert into the medial epicondyle of the humerus. In two of these instances, a tendinous band from this muscular slip passed proximally to gain attachment to the capsule of the shoulder joint.

Instances have been described (e.g. Parsons 1898 ; Perrin 1871) of muscular fibres from the inferior border of the pars sternocostalis of m. pectoralis major passing across the axilla and fusing with the inferior border of m. latissimus dorsi. Perrin (1871) gives the incidence of this " axillary arch " as seventeen per cent of fifty-eight subjects.

The pars clavicularis and the pars sternocostalis of m. pectoralis major were, in each dissection, of approximately uniform thickness, but any pars abdominalis was much thinner.

The direction and insertion of the fibres were as in brachiators. Perrin (1871) has described a case of the proximal part of the tendon of insertion splitting and

gaining attachment to both the medial and lateral margins of the intertubercular groove, thus forming an arch through which passed the caput longum of *m. biceps brachii*.

TABLE 4
Variation in the caudal limit of origin of *m. pectoralis major* (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which caudal limit of origin was from ribs				
	Present study	Literature*	5	6	7	8	9
Quadrupeds ..	26	95	—	—	17.4	78.5	4.1
Semibrachiators	5	13	44.4	50.0	5.6	—	—
Brachiators ..	6	40	10.9	32.6	43.5	13.0	—
Man	3	—	—	—	100.0	—	—

Significance of differences in mean caudal limit of origin of *m. pectoralis major*: Man, Brachiators, Semibrachiators and Quadrupeds: $P < 0.001$; Man and Brachiators: $P = 0.01-0.001$; Man and Semibrachiators: $P < 0.001$; Man and Quadrupeds: $P < 0.001$; Brachiators and Semibrachiators: $P < 0.001$; Brachiators and Quadrupeds: $P < 0.001$; Semibrachiators and Quadrupeds: $P < 0.001$.

* Beattie 1927; Bischoff 1870; Broca 1869; Champneys 1872; Chapman 1880; Church 1861; Duvernoy 1855; Gratiolet & Alix 1866; Huntington 1903; Kohlbrugge 1897; MacDowell 1910; Matsuo 1960; Michaelis 1903; Miller 1952; Mivart 1865; Pagenstecher 1867; Patterson 1942; Pira 1913; Polak 1908; Primrose 1899; Raven 1950; Robertson 1944; Sandifort 1841; Sommer 1907; Sonntag 1923; Stewart 1936; Sullivan & Osgood 1927; Tschachmachtschjan 1911; Zuckercandl, 1910.

M. pectoralis minor

General description: *M. pectoralis minor* is triangular and is completely concealed by *m. pectoralis major*. It takes origin by fleshy fibres from the upper part of the ventral aspect of the thoracic cage. The fibres pass cranio-laterally to form a short flat tendon which gains a variable insertion in the neighbourhood of the shoulder joint.

Principal contrasts between locomotor groups: (Pls. 1-7 and Table 5): In quadrupeds, this muscle is more extensive and is directed more cranially than in other locomotor groups. Its principal characters are similar in semibrachiators, brachiators and man.

Variation: (a) *quadrupeds:* (Pl. 1, fig. 2 and Pl. 2, fig. 6): *M. pectoralis minor* arose from the sternebrae and from the medial ends of certain costal cartilages—usually, the second to the sixth (Table 5).

The fibres passed in a somewhat oblique, but mostly cranial direction, and inserted mainly into the capsule of the shoulder joint.

In all our New World quadrupeds, the most medial fibres were attached to the tip of the coracoid process and the fascia linking this to the capsule of the shoulder joint, while the most lateral fibres were attached to the greater tuberosity. Lander (1918) reported that in a single specimen of *Cebus*, the complete insertion of *m.*

pectoralis minor was into the joint-capsule, but that in a specimen of *Hapale* (= *Callithrix*), it was entirely into the "head of the humerus". Windle (1886a) reported on a specimen of *Hapale* (= *Callithrix*), where m. pectoralis minor inserted into the capsule of the shoulder joint and into the tendon of m. pectoralis major. In a specimen of *Midas* (= *Leontocebus*), Windle (1886b) found m. pectoralis minor to gain insertion into the coracoid process, the joint-capsule and the tendon of m. pectoralis major.

In all Old World specimens, although most fibres inserted into the capsule of the shoulder joint, a few of the more lateral constantly gained attachment to the greater tuberosity. Matsuo (1960) in a series of fifty specimens of *Macaca cyclopsis* found that in addition to this insertion, the more medial fibres of m. pectoralis minor gained attachment to the tip of the coracoid process. Champneys (1872) and Zuckercandl (1910) recorded similar variations in *Papio* and *Cercopithecus* respectively. In a specimen of *Cynopithecus*, Patterson (1942) found the most medial fibres to form a small tendon, which, distinct from the main insertion, gained attachment to the coracoid process. In two specimens of *Papio*, Lander (1918) found the insertion of m. pectoralis minor to be confined to the capsule of the shoulder joint.

(b) *semibrachiators*: (Pl. 3, fig. 10 and Pl. 4, fig. 14) : M. pectoralis minor usually arose from the second, third and fourth costal cartilages (Table 5).

The direction of the fibres, although predominantly cranial, was somewhat more oblique than in quadrupeds. Except in one of two specimens of *Colobus*, the muscle was inserted into the greater tuberosity, the joint-capsule, the fascia connecting the capsule with the coracoid process and into the tip of the process itself. In the exceptional case, the insertion was restricted to the greater tuberosity and the joint-capsule. Polak (1908) in a specimen of *Colobus*, found the insertion of m. pectoralis minor to be wholly capsular. In a specimen of *Rhinopithecus*, Patterson (1942) found that the most medial fibres inserted by a small independent tendon into the coracoid process.

(c) *brachiators*: (Pl. 5, fig. 18 and Pl. 6, fig. 22) : The muscle arose most frequently from three ribs (Table 5). The fibres did not extend medially on to the costal cartilages but their general direction was similar to that in semibrachiators.

In the available specimens of *Hylobates* and *Symphalangus*, the fibres inserted into the coracoid process and the ligamentum coracoacromiale. Hepburn (1892) described a specimen of *Hylobates* in which m. pectoralis minor inserted into the coracoid process, the adjoining part of the clavicle and the tendon common to m. coracobrachialis and the caput breve of m. biceps brachii. Stewart (1936) described a further specimen with an insertion into the coracoid process, the adjacent parts of the clavicle and the ligamentum coracoacromiale.

In the available specimen of *Pongo*, m. pectoralis minor was inserted into the coracoid process, the capsule of the shoulder joint and the intervening fascia. In the single specimens dissected by Bischoff (1870) and Hepburn (1892), the insertion was restricted to the coracoid process. Primrose (1899) found that the muscle was inserted not only into the coracoid, but also into the adjacent parts of the clavicle and acromion.

In both our specimens of *Pan*, the insertion extended from the coracoid process to the joint-capsule. Gratiolet and Alix (1866) found in their specimen, an additional insertion into the ligamentum coracoacromiale. More restricted insertions have also been described. On the one hand Hepburn (1892) encountered a specimen with m. pectoralis minor inserting into the coracoid process only and Keith (1899) found a similar insertion in seven (thirty-nine per cent) of eighteen dissections. On the other hand, Champneys (1872) and Sutton (1883) described specimens of *Pan* with the insertion confined to the joint-capsule. Humphry (1867) recorded an instance in which most fibres inserted into the capsule but some of the most lateral gained attachment to the greater tuberosity.

In the three specimens of *Gorilla* described by Stewart (1936) and Raven (1950), the insertion of m. pectoralis minor was restricted to the coracoid process. A similar insertion was found in a total of thirteen specimens described by Hepburn (1892), Keith (1899) and Lander (1918).

(d) *man*: (Pl. 7, fig. 26): The origin and direction of m. pectoralis minor (Table 5) corresponded with the arrangement typical of brachiators. Its tendon was inserted into the tip of the coracoid process only. Macalister (1867) described a subject where m. pectoralis minor inserted into the coracoid process, into the capsule of the shoulder joint and the rim of the glenoid fossa. Ciardi-Dupré (1949) found that in a series of twenty-four subjects, m. pectoralis minor in one instance inserted into the coracoid process, the joint-capsule and the intervening connective tissue ; in a second into the capsule only, while in a third, the tendon divided, the medial part gaining attachment to the lateral end of the clavicle and the lateral part inserting into the capsule.

M. pectoralis abdominalis

General description: This elongated muscle takes origin from certain costal cartilages distal to the caudal limit of m. pectoralis major. Some of the most superficial fibres blend with the aponeurosis covering m. obliquus externus abdominis and m. rectus abdominis. The fibres of m. pectoralis abdominalis pass cranio-laterally and converge upon a short, flattened tendon which inserts into the capsule of the shoulder joint distal to, and conjoined with, the tendon of m. pectoralis minor.

Principal contrasts between locomotor groups: (Pls. 1-7 and Table 6): In quadrupeds, m. pectoralis abdominalis is relatively big and the direction of its fibres is predominantly cranial.

In semibrachiators, the muscle is smaller and its fibres are directed more obliquely.

In brachiators and man, m. pectoralis abdominalis does not normally exist as a distinct unit.

Variation: (a) *quadrupeds*: (Pl. 1, fig. 2 and Pl. 2, fig. 6) : In this group, the muscle generally took origin from the eighth to eleventh costal cartilages (Table 6). The most cranial fibres blended near their origin with the most caudal fibres of m. pectoralis major (pars sternocostalis). The muscle passed cranially and somewhat laterally to its insertion.

TABLE 5
Variation in the origin of *m. pectoralis minor* (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from ribs			
	Present study	Literature*	1	2	3	4
Quadrupeds ..	26	108	6.7	79.9	13.4	—
Semibrachiators	5	21	3.8	73.1	23.1	—
Brachiators ..	6	41	4.2	44.7	42.6	8.5
Man	3	100	4.9	58.2	35.9	1.0

Significance of differences in mean cranial limit of origin of *m. pectoralis minor*: Man, Brachiators, Semibrachiators and Quadrupeds: $P < 0.001$; Man and Brachiators: $P = 0.1-0.05$; Man and Semibrachiators: $P = 0.3-0.2$; Man and Quadrupeds: $P < 0.001$; Brachiators and Semibrachiators: $P = 0.02-0.01$; Brachiators and Quadrupeds: $P < 0.001$; Semibrachiators and Quadrupeds: $P = 0.3-0.2$.

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs					
	Present study	Literature*	3	4	5	6	7	8
Quadrupeds ..	26	108	0.7	—	12.7	56.7	20.9	9.0
Semibrachiators	5	21	3.9	65.4	19.2	11.5	—	—
Brachiators ..	6	41	8.5	40.4	46.8	—	4.3	—
Man	3	100	—	21.4	73.8	4.8	—	—

Significance of differences in mean caudal limit of origin of *m. pectoralis minor*: Man, Brachiators, Semibrachiators and Quadrupeds: $P < 0.001$; Man and Brachiators: $P = 0.02-0.01$; Man and Semibrachiators: $P = 0.01-0.001$; Man and Quadrupeds: $P < 0.001$; Brachiators and Semibrachiators: $P = 0.6-0.5$; Brachiators and Quadrupeds: $P < 0.001$; Semibrachiators and Quadrupeds: $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which							
	Present study	Literature*	2	3	4	5	6	7	8	

Significance of differences in mean numbers of ribs spanned by *m. pectoralis minor*: Man, Brachiators, Semibrachiators and Quadrupeds: $P < 0.001$; Man and Brachiators: $P < 0.001$; Man and Semibrachiators: $P = 0.05-0.02$; Man and Quadrupeds: $P < 0.001$; Brachiators and Semibrachiators: $P = 0.2-0.1$; Brachiators and Quadrupeds: $P < 0.001$; Semibrachiators and Quadrupeds: $P < 0.001$.

* Anson, Lindsay & McDonald 1938; Beattie 1927; Broca 1869; Campbell 1937; Champneys 1872; Chapman 1878; Dobson 1881; Gratiolet & Alix 1866; Hepburn 1892; Huntington 1903; Kallner 1956; Kohlbrugge 1897; MacDowell 1910; Matsuo 1960; Miller 1952; Mivart 1865; Pagenstecher 1867; Patterson 1942; Pira 1913; Polak 1908; Primrose 1899; Raven 1950; Robertson 1944; Sandifort 1841; Sommer 1907; Sonntag 1922, 1923, 1924; Stewart 1936; Sullivan & Osgood 1927; Sutton 1883; Tschachmachtschjan 1911; Windle 1886a; Zuckercandl 1910.

(b) *semibrachiators*: (Pl. 3, fig. 10, and Pl. 4, fig. 14) : *M. pectoralis abdominalis* usually arose from the two costal cartilages distal to the caudal edge of *m. pectoralis major* (pars sternocostalis) to which, however, it was not joined (Table 6). In one of three specimens of *Lagothrix* described by Robertson (1944), there was no *m. pectoralis abdominalis*, but the origin of *m. pectoralis major* extended two ribs caudal to the level typical of semibrachiators. In a single specimen of *Rhinopithecus*, Patterson (1942) found that the adjacent borders of *m. pectoralis major* and *m. pectoralis abdominalis* were fused near their origin. Tschachmachtschjan (1911), in a specimen of *Semnopithecus* (= *Presbytis*) *cephalopterus*, found *m. pectoralis abdominalis* to be fused with *m. panniculus carnosus*, the combined origin extending from the sixth to the tenth ribs.

TABLE 6
Variation in the origin of *m. pectoralis abdominalis*
(Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from ribs				
	Present study	Literature*	5	6	7	8	9
Quadrupeds ..	26	86	—	—	13.4	70.5	16.1
Semibrachiators	5	10	13.3	66.7	20.0	—	—

Significance of differences in mean cranial limit of origin of *m. pectoralis abdominalis* : Quadrupeds and Semibrachiators : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs						
	Present study	Literature*	5	6	7	8	9	10	11
Quadrupeds ..	26	86	—	—	—	—	8.0	24.1	67.9
Semibrachiators	5	7	16.7	16.7	50.0	16.7	—	—	—

Significance of differences in mean caudal limit of origin of *m. pectoralis abdominalis* : Quadrupeds and Semibrachiators : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which ribs were spanned				
	Present study	Literature*	1	2	3	4	5
Quadrupeds ..	26	86	—	16.1	16.1	62.5	5.3
Semibrachiators	5	7	50.0	41.7	8.3	—	—

Significance of differences in mean numbers of ribs spanned by *m. pectoralis abdominalis* : Quadrupeds and Semibrachiators : $P < 0.001$.

* Beattie 1927 ; Huntington 1903 ; Kohlbrugge 1897 ; MacDowell 1910 ; Matsuo 1960 ; Mivart 1865 ; Patterson 1942 ; Robertson 1944 ; Tschachmachtschjan 1911.

The muscle was narrower than in quadrupeds, as confirmed by Zuckercandl (1910) who noted in a specimen of *Ateles*, the width of origin of m. pectoralis abdominalis as approximately one eighth only of that observed in a specimen of *Macaca* of equivalent gross size.

The direction of the fibres and their method of insertion were, in all instances, as in quadrupeds.

(c) and (d) *brachiators and man*: M. pectoralis abdominalis was not found as a distinct unit in any specimens of the Hominoidea.

Perrin (1871) and Harvey (1907) described individual human subjects in which a muscular slip, possibly homologous with m. pectoralis abdominalis, took origin immediately distal to and separate from the inferior border of m. pectoralis major and inserted into either the coracoid process (Perrin 1871) or both the coracoid process and the capsule of the shoulder joint (Harvey 1907). A minor manifestation of this variation was described by Harvey (1907) who recorded that in seventeen (thirty-three per cent) of fifty-one subjects, the inferior fibres of the pars sternocostalis, instead of participating in the formation of the main tendon of m. pectoralis major, formed a small separate tendon that passed deeply to gain insertion into the coracoid process.

It has also been suggested (e.g. Lander 1918 ; Howell and Straus 1933) that the fibres normally regarded as constituting the pars abdominalis of m. pectoralis major, are homologous with m. pectoralis abdominalis.

TABLE 7
Variation in the caudal limit of the pectoral mass (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs						
	Present study	Literature*	5	6	7	8	9	10	11
Quadrupeds ..	26	86	—	—	—	—	8.0	24.1	67.9
Semibrachiators	5	9	14.3	14.3	57.1	14.3	—	—	—
Brachiators ..	6	40	10.9	32.6	43.5	13.0	—	—	—
Man	3	0	—	—	100.0	—	—	—	—

Significance of differences in mean caudal limit of origin of the pectoral mass : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P = 0.01-0.001$; Man and Semibrachiators : $P = 0.3-0.2$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P = 0.7-0.6$; Brachiators and Quadrupeds : $P < 0.001$; Semibrachiators and Quadrupeds : $P < 0.001$.

* Beattie 1927 ; Bischoff 1870 ; Broca 1869 ; Champneys 1872 ; Chapman 1880 ; Church 1861 ; Duvernoy 1855 ; Gratiolet & Alix 1866 ; Huntington 1903 ; Kohlbrugge, 1897 ; MacDowell 1910 ; Matsuo 1960 ; Michaelis 1903 ; Miller 1952 ; Mivart 1865 ; Patterson 1942 ; Pira 1913 ; Polak 1908 ; Primrose 1899 ; Raven 1950 ; Robertson 1944 ; Sandifort 1841 ; Sommer 1907 ; Sonntag 1923 ; Stewart 1936 ; Sullivan & Osgood 1927 ; Tschachmachtschjan 1911 ; Zuckercandl 1910.

The pectoral mass (Pls. 1-7 and Table 7)

M. pectoralis major, m. pectoralis minor and m. pectoralis abdominalis appear to form a single functional unit described by Huntington (1903) as the "pectoral

mass". There is a marked contrast between locomotor groups in the extent of its origin. In quadrupedal monkeys, the origin is relatively long and extends caudally as far as the tenth or eleventh costal cartilage. In semibrachiators, the origin is shorter, extending caudally as far as the sixth or seventh costal cartilage. In brachiators, the caudal limit is similar to that in semibrachiators. But in the apes, the thoracic cage is relatively broader than in monkeys (e.g. Schultz 1930) and consequently the length of origin of the pectoral mass, relative to that of its fibres, is even less.

The form and disposition of the pectoral mass are, in man, similar to those of brachiators.

M. latissimus dorsi

General description: *M. latissimus dorsi* is broad and triangular, its fibres lying superficially and covering much of the dorsal aspect of the caudal part of the trunk. It arises by tendinous fibres from the spines and supraspinous ligaments of the lower thoracic vertebrae, and from the fascia thoracolumbalis. The fibres from the vertebral spines become fleshy almost immediately, while those from the fascia thoracolumbalis become fleshy at approximately the caudal edge of the thoracic cage. All fibres pass cranially and to some extent ventro-laterally, and converge towards the posterior axillary wall. They gain attachment to a short, narrow tendon which is inserted into the middle of the medial lip of the inter-tubercular groove.

Principal contrasts between locomotor groups: (Pls. 1-7 and Table 8): In quadrupeds, *m. latissimus dorsi* is thin and its origin is restricted to the dorsum of the trunk. Its fibres pass obliquely in a cranio-ventral direction.

In semibrachiators, the muscle is appreciably thicker, and its origin extends further ventrally than in quadrupeds. The fibres are also directed more cranially.

In brachiators, the muscle is even thicker and its origin extends still further in a ventral direction. The fibres are directed almost entirely cranially.

In man, the principal characters of *m. latissimus dorsi* correspond with those found in quadrupeds.

Variation: (a) quadrupeds: (Pl. 1, fig. 3, and Pl. 2, fig. 7): Variations in the cranial limit of origin of *m. latissimus dorsi* are summarized in Table 8. This limit varied in the New World species between the twelfth thoracic and first lumbar spines, and in the Old World species between the second and third lumbar spines.

Hill (1960) mentioned that in a single specimen of *Callicebus*, the most ventral fibres of *m. latissimus dorsi* gained attachment to the iliac crest. Patterson (1942) reported a similar variation in *Cynopithecus*.

The muscle was uniformly thin and fleshy slips, usually arising from the last two ribs, blended with its deep surface as the fibres swept cranio-ventrally.

The insertion of the muscle scarcely differed from that characteristic of the Anthropoidea as a whole, but in three of the five specimens of *Cercopithecus* and in the single specimens of *Papio* and *Comopithecus*, fleshy fibres were detached from the muscle close to the base of its tendon, and blended with those of *m. teres major*. Schuck (1912) found a similar variation in two specimens of *Cebus*, three

of *Macaca*, one of *Cercocebus*, two of *Papio*, one of *Comopithecus* and five of *Cercopithecus*.

In an examination of fifteen New World monkeys, of which all except five specimens of *Ateles* were quadrupeds, Dzwonkowski (1937) found that the characters of m. latissimus dorsi were, on average, as described in the present study.

(b) *semibrachiators*: (Pl. 3, fig. 11 and Pl. 4, fig. 15) : The cranial limit of origin of m. latissimus dorsi was usually the eighth thoracic spine (Table 8). The more caudal fibres gained attachment through the fascia thoracolumbalis to the lumbar vertebrae, to the sacrum and to the short iliac crest. Prominent bundles of fibres also arose from the lateral aspect of some of the lowermost ribs (Table 8). These fibres formed the ventral edge of the muscle and extended to the mid-axillary line.

The direction of the most ventral fibres was always more nearly cranial, and the muscle was appreciably thicker than in quadrupeds.

In the dissected specimens, the insertion did not vary. Patterson (1942), however, found that in one specimen of *Rhinopithecus* a "large fleshy slip" became detached from m. latissimus dorsi and fused with m. teres major.

In his extensive study of m. latissimus dorsi, Dzwonkowski (1937) drew no specific attention to this muscle in semibrachiators, but his diagrams of *Ateles* show that it is bigger and more extensive than in quadrupeds.

(c) *brachiators*: (Pl. 5, fig. 19 and Pl. 6, fig. 23) : The cranial limit of origin of m. latissimus dorsi was most frequently the spine of the ninth thoracic vertebra (Table 8). In all our specimens, the fibres gained attachment through the fascia thoracolumbalis to the lumbar vertebrae and sacrum. In the specimens of *Hylobates* and *Symphalangus*, the muscle had additional attachment through this fascia to the entire external lip of the iliac crest. In these species, fleshy fibres forming the ventral part of the muscle also arose from the aponeurosis of m. obliquus externus abdominis and from the lower six ribs. In the dissections of *Pan* and *Pongo*, and in those of *Gorilla* studied by Stewart (1936) and Raven (1950), the muscle was attached through the fascia thoracolumbalis to the medial half of the iliac crest (which in these genera is relatively longer than in *Hylobates* and *Symphalangus*) and by fleshy fibres to its lateral half. Cranio-ventral to this, several slips arose from the lower ribs, interdigitating with the origin of m. obliquus externus abdominis (Table 8).

In all specimens, the ventral border of m. latissimus dorsi extended beyond the mid-axillary line.

The muscle was conspicuously thicker than in semibrachiators, the development of its ventral border being especially prominent, and the fibres in this region passing almost directly cranially.

In the specimen of *Pongo*, and in five further specimens described by Church (1861), Chapman (1880), Hepburn (1892), Primrose (1899) and Schuck (1912), some fibres became detached from the cranial edge of the main mass of the muscle close to its musculotendinous junction, and were inserted along with those of m. teres major. A corresponding variation in five out of six specimens of *Pan* was reported by Hepburn (1892), Schuck (1912) and Sonntag (1923).

The pattern of insertion did not vary from that described for the Anthropeidea in general.

From a study of four specimens of *Hylobates*, five of *Pan* and one of *Pongo*, Dzwonkowski (1937) concluded that in apes, *m. latissimus dorsi* is bigger and more strongly developed than in monkeys.

(d) *man*: (Pl. 7, fig. 27) : The fibres of *m. latissimus dorsi* took tendinous origin from the vertebrae inferior to the sixth thoracic, and from the extreme postero-medial end of the iliac crest. Standard anatomical texts indicate that in contrast to the specimens dissected in the present study, some fibres may take fleshy origin from the extreme medial end of the iliac crest.

Fleshy slips took origin from the lowest three ribs to blend with the fibres on the deep surface of the muscle ; they did not, however, form its anterior margin. The standard texts mention an occasional further slip arising from the inferior angle of the scapula.

TABLE 8
Variation in the origin of *m. latissimus dorsi* (Anthropeidea).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was at the level of						
	Present study	Literature*	T.4	T.5	T.6	T.7	T.8	T.9	T.10
Quadrupeds ..	26	33	42.4	18.6	8.5	20.3	10.2	—	—
Semibrachiators	5	8	—	—	7.7	23.1	46.1	15.4	7.7
Brachiators ..	6	32	—	—	—	5.3	21.0	55.3	18.4
Man	3	0	—	—	100.0	—	—	—	—

Significance of differences in mean cranial limit of origin of *m. latissimus dorsi* : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P < 0.001$; Man and Semibrachiators : $P < 0.001$; Man and Quadrupeds : $P = 0.01-0.001$; Brachiators and Semibrachiators : $P = 0.01-0.001$; Brachiators and Quadrupeds : $P < 0.001$; Semibrachiators and Quadrupeds : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which slips took origin from							
	Present study	Literature*	0	1	2	3	4	5	6	7
Quadrupeds ..	26	36	43.5	17.7	19.4	9.7	8.1	—	—	1.6
Semibrachiators	5	7	—	—	8.3	25.0	8.3	41.7	16.7	—
Brachiators ..	6	33	12.8	2.6	7.7	17.9	10.3	20.5	23.1	5.1
Man	3	0	—	—	—	100.0	—	—	—	—

Significance of differences in mean numbers of slips taking origin from the ribs : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P = 0.02-0.01$; Man and Semibrachiators : $P = 0.01-0.001$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P = 0.4-0.3$; Brachiators and Quadrupeds : $P < 0.001$; Semibrachiators and Quadrupeds : $P < 0.001$.

* Beattie 1927 ; Biscoff 1880 ; Campbell 1937 ; Champneys 1872 ; Duvernoy 1855 ; Gratiolet & Alix 1866 ; Hepburn 1892 ; Kallner 1956 ; Kohlbrugge 1897 ; MacDowell 1910 ; Miller 1952 ; Patterson 1942 ; Pira 1913 ; Polak 1908 ; Primrose 1899 ; Raven 1950 ; Schuck 1912 ; Sommer 1907 ; Sonntag 1922, 1924 ; Stewart 1936 ; Sullivan & Osgood 1927.

M. latissimus dorsi was thin and narrow and was directed more anteriorly (=ventrally) than in brachiators or semibrachiators.

The insertion was similar to that characteristic of monkeys and apes. Macalister (1867) described an instance of *m. latissimus dorsi* inserting by a double tendon, *m. teres major* being absent. Curnow (1873) noted the occurrence of two muscular bundles arising from *m. latissimus dorsi* close to its musculotendinous junction, and blending with *m. teres major* and the *caput longum* of *m. triceps brachii* respectively. The muscle was further linked to the scapula by a tendinous band.

M. dorsoepitrochlearis

General description: *M. dorsoepitrochlearis* is a small, straplike muscle whose fibres take origin from the junction between the fleshy fibres of *m. latissimus dorsi* and those of its tendon of insertion. The fibres pass down the dorso-medial aspect of the arm and are inserted into bony points and fascial sheets around the elbow.

Principal contrasts between locomotor groups: (Pls. 1–7): In quadrupeds, *m. dorsoepitrochlearis* is inserted distal to the elbow joint.

In semibrachiators, whereas part of the muscle inserts proximal to the elbow joint, part may also be inserted distally.

In brachiators, the insertion is entirely proximal to the elbow joint.

M. dorsoepitrochlearis is not normally found in man.

Variation: (a) *quadrupeds:* (Pl. 1, fig. 1 and Pl. 2, fig. 7): No variations in the origin of *m. dorsoepitrochlearis* were encountered. The fibres of origin were closely bound to the epimysium on the axillary border of *m. subscapularis*.

The most medial fibres gained a tendinous insertion into the dorsal aspect of the medial epicondyle. The most lateral were attached to the medial aspect of the olecranon, while the intermediate fibres formed a tendinous slip which passed distally to blend with the fascia covering the extensor aspect of the forearm. In the specimens of *Macaca*, *Papio*, *Comopithecus* and *Mandrillus*, this tendinous slip was relatively more prominent than in other genera. In *Callithrix*, Beattie (1927) found *m. dorsoepitrochlearis* to be inserted only into the olecranon and into the extensor fascia. A similar pattern of insertion was reported by Patterson (1942) in his specimen of *Cynopithecus*. Breinl (1958) noted that in one of three specimens of *Papio*, *m. dorsoepitrochlearis* inserted into the tendon of *m. triceps brachii*, which in turn, gained attachment both to the olecranon and to the antebrachial extensor fascia.

(b) *semibrachiators:* (Pl. 3, fig. 11 and Pl. 4, fig. 15): The origin and general disposition of *m. dorsoepitrochlearis* agreed with the pattern common to all groups of the Anthropoidea. But in our specimens of *Alouatta*, *Lagothrix* and *Ateles*, a strong fibrous band connected the point of origin of *m. dorsoepitrochlearis* from the musculotendinous junction of *m. latissimus dorsi*, with the neck of the scapula. A similar band was found by Campbell (1937) in four specimens of *Ateles* and in one of two dissections of *Alouatta*.

In our specimens of *Ateles* and *Lagothrix*, the lateral fibres were inserted into the medial intermuscular septum, and the medial fibres into the medial epicondyle.

In the specimen of *Alouatta*, all fibres were attached through a short tendon to the dorsal aspect of the medial epicondyle. In both specimens of *Colobus*, the medial fibres gained attachment to the medial epicondyle and the lateral ones to the medial aspect of the olecranon. Polak (1908) described a specimen of *Colobus* in which m. dorsoepitrochlearis inserted into the medial intermuscular septum and into the medial epicondyle. Patterson (1942), in a specimen of *Rhinopithecus*, found the muscle to be inserted exclusively into the medial aspect of the olecranon.

(c) *brachiators*: (Pl. 5, fig. 17 and Pl. 6, fig. 21): In our dissections, and in two specimens of *Gorilla* (Raven 1950), a prominent fibrous band linked the line of origin of m. dorsoepitrochlearis with the fascia covering the axillary border of m. subscapularis. In the specimens of *Hylobates* and *Symphalangus*, the lateral fibres of m. dorsoepitrochlearis inserted into the fascia covering m. triceps brachii and into the distal part of the medial intermuscular septum. The medial fibres were attached to the dorsal surface of the medial epicondyle. In a specimen of *Hylobates*, Chapman (1900) found the insertion of m. dorsoepitrochlearis to be restricted to the medial epicondyle, while Gronroos (1902) reported an insertion entirely into the medial intermuscular septum.

In our specimen of *Pongo*, all fibres of m. dorsoepitrochlearis were inserted into the fascia covering m. triceps brachii and into the proximal part of the medial intermuscular septum. Church (1861) and Sullivan and Osgood (1927) described specimens in which a slip from m. dorsoepitrochlearis inserted by tendinous fibres into the dorsal aspect of the medial epicondyle. Kallner (1956) described two specimens of this ape in which m. dorsoepitrochlearis inserted exclusively into the medial intermuscular septum.

In the specimens of *Pan*, m. dorsoepitrochlearis inserted into the medial epicondyle and supracondylar ridge. Bischoff (1870) described an instance of m. dorsoepitrochlearis being inserted into the fascia covering m. triceps brachii.

In the two specimens of *Gorilla* described by Raven (1950), m. dorsoepitrochlearis inserted by a stout tendon into the medial epicondyle.

(d) *man*: M. dorsoepitrochlearis was not found in any of the three subjects dissected in the present study. But a number of authors (Macalister 1867; Testut 1899; Wood 1867) have noted its occasional representation by a fibrous band, sometimes containing muscle fibres, extending from the musculotendinous junction of m. latissimus dorsi to the deep fascia of the arm. Testut (1884, cit Breinl 1958) reported that M. dorsoepitrochlearis exists in this form in five per cent of cases.

M. teres major

General description: M. teres major is an elongated rectangular muscle which arises by fleshy fibres from a ridged elliptical area around the inferior angle of the scapula, and by tendinous fibres from the adjoining part of the lateral margin. The fibres pass laterally and to some extent cranially, to gain a linear insertion into the entire length of the medial lip of the intertubercular groove. The intermediate part of the insertion lies medial to the attachment of the tendon of m. latissimus dorsi.

Principal contrasts between locomotor groups: (Pls. 1-7) : The main features of this muscle are similar in each of the four locomotor groups.

Variation: (a) *quadrupeds:* (Pl. 1, fig. 3 and Pl. 2, fig. 8) : In this group, the fleshy angular origin was big and the tendinous attachment extended over the adjacent two-thirds of the lateral border of the scapula. The general characters of the muscle showed no noteworthy variations, except, that as already noted (p. 574), in certain instances fleshy fibres were received from m. latissimus dorsi.

(b) *semibrachiators:* (Pl. 3, fig. 12 and Pl. 4, fig. 15) : The area of fleshy origin around the inferior angle of the scapula was conspicuously smaller than in quadrupeds, and the tendinous origin extended over only the adjacent one quarter of the lateral border. The remaining characters of the muscle did not deviate from the pattern characteristic of other groups of the Anthropeidea.

(c) *brachiators:* (Pl. 5, fig. 19 and Pl. 6, fig. 23) : As in semibrachiators, the fleshy angular origin was notably smaller than in quadrupeds, but the tendinous attachment extended over the adjoining half of the lateral border of the scapula. The remaining characters showed no noteworthy variations, but, as already noted (p. 575), in our specimen of *Pongo*, as in other recorded instances in the Pongidae, the muscle received fibres from m. latissimus dorsi.

(d) *man:* (Pl. 7, fig. 27) : The fleshy origin from the inferior angle of the scapula appeared relatively more extensive than in brachiators or in semibrachiators, but the tendinous origin extended for only a short distance along the lateral border. The remaining features of the muscle did not differ from the pattern characteristic of the Anthropeidea.

Muscles responsible for raising the arm

M. deltoideus

General description: M. deltoideus is a thick triangular muscle extending from the lateral parts of the shoulder girdle to the shaft of the humerus. It comprises three divisions (pars claviculæ, pars acromialis and pars spinalis) that arise respectively from the lateral part of the ventral aspect of the clavicle, from the lateral aspect of the acromion and an aponeurosis overlying this part of the muscle, and from the caudal edge of the scapular spine. The pars acromialis is pennate, its superficial fibres inserting by a short stout tendon into the distal part of the deltoid tuberosity, its deep fibres gaining a fleshy attachment more proximally. The pars claviculæ and the pars spinalis converge to be inserted by short tendinous fibres into the sides of the tendon of the pars acromialis and into the ventral and dorsal margins of the deltoid tuberosity.

Principal contrasts between locomotor groups: (Pls. 1-7) : In quadrupeds, m. deltoideus is small, its three heads are clearly separated and insert into the humerus approximately a third of the way between the shoulder and elbow.

In semibrachiators, the muscle is relatively bigger and the separation between the heads is less marked. The muscle is inserted near the midpoint of the humerus.

In brachiators, *m. deltoideus* reaches its maximum development, its three heads coalescing to form a single unit which inserts into the humerus some two-thirds of the way down the shaft.

In man, the muscle is well developed. Its three heads are joined to form a single unit, which, as in semibrachiators, inserts half-way along the humerus.

Variation: (a) quadrupeds: (Pl. 1, figs. 1 and 3 and Pl. 2, figs. 5 and 7) : The *pars clavicularis* usually took origin from the lateral third of the clavicle. But in one of the five specimens of *Macaca*, the origin was from the lateral three-quarters of the bone, while in the remaining four specimens, and in the five specimens of *Cercopithecus*, it was from the lateral half.

No variations of the *pars acromialis* were recorded.

The *pars spinalis* originated from the lateral half of the scapular spine. In the specimen of *Cacajao*, the most dorsal fibres of the *pars spinalis* took origin from the fascia covering *m. infraspinatus*. A similar origin, although extending much closer to the inferior scapular angle, was found in all Old World quadrupeds.

In the specimens of *Aotes*, *Callithrix*, *Leontocebus*, *Papio*, *Comopithecus* and *Mandrillus* and in one of the two of *Pithecia*, the three heads of the muscle were separated by triangular spaces containing loose areolar tissue. In the specimens of *Cacajao*, *Macaca* and *Cercopithecus* and in a specimen of *Cynopithecus* described by Patterson (1942), the heads were joined by fibrous raphes.

In the specimens of *Callicebus* and *Saimiri* and in one of *Pithecia*, the *pars clavicularis* was joined to the *pars acromialis* by a fibrous raphe, while a triangular space filled with loose areolar tissue intervened between the *pars acromialis* and the *pars spinalis*.

The insertion of *m. deltoideus* agreed with the pattern typical of the Anthro-poidea as a whole. But in *Callithrix* (Beattie 1927), while the *pars acromialis* and the *pars clavicularis* were inserted into the distal part of the deltoid tuberosity, the *pars spinalis* passed deeply, to be inserted proximally into the lateral lip of the intertubercular groove.

(b) semibrachiators: (Pl. 3, figs. 9 and 11 and Pl. 4, figs. 13 and 15) : In *Alouatta*, *Ateles* and *Lagothrix*, the *pars clavicularis* arose from the lateral third of the clavicle but in *Colobus*, from the lateral two-thirds. The origin of the *pars acromialis* showed no noteworthy variations, but the *pars spinalis* took origin not only from the lateral half of the scapular spine, but also from the fascia covering *m. infraspinatus*. They thereby gained an indirect attachment to the infraspinous fossa along the line separating *m. infraspinatus* from *m. teres major*.

Although in our material, adjacent heads of the muscle were joined by fibrous raphes, Patterson (1942) in his specimen of *Rhinopithecus*, found the *pars acromialis* fused with the *pars spinalis*.

The pattern of insertion conformed to that typical of the Anthropoidea.

(c) brachiators: (Pl. 5, figs. 17 and 19 and Pl. 6, figs. 21 and 23) : In all available specimens and in those of *Gorilla* described by Raven (1950), the *pars clavicularis* arose from the lateral third of the clavicle. In three specimens of *Pongo* described by Sullivan and Osgood (1927) and Kallner (1956), the origin extended over the

lateral half of the bone. Sonntag (1924) also reported this to be typical of *Pongo*.

No variations have been recorded in the origin of the pars acromialis.

The pars spinalis took origin as in semibrachiators, but in addition, the extreme caudal fibres of the muscle had a tendinous attachment to the lateral border of the scapula.

Adjacent heads were consistently joined by fibrous raphes.

In addition to the insertion into the deltoid tuberosity, a strong fibrous expansion arising from the tendon gained attachment to the fascia covering m. brachialis and m. triceps brachii, a number of its fibres passing between these muscles to be inserted into the humerus proximal to the lateral supracondylar process. In the specimens of *Gorilla* figured by Raven (1950) this part of the insertion was exceptionally prominent. In a specimen of *Pongo*, Church (1861) found that the pars acromialis inserted by a separate tendon into the humerus distal to the deltoid tuberosity.

(d) *man*: (Pl. 7, figs. 25 and 27) : The origins of the pars clavicularis and the pars acromialis were similar to those found in brachiators. But, in contrast, the origin of the pars spinalis was, as in quadrupeds, restricted to the lateral half of the scapular spine.

The proximal parts of adjacent heads of the muscle were separated by loose areolar tissue which was replaced more distally by fibrous raphes.

The insertion was similar to that seen in brachiators, except that the expansion arising from the tendon of insertion was small. It blended imperceptibly with the fascia covering m. brachialis, and had no direct attachment to the humerus.

M. trapezius

General description: M. trapezius is triangular having a linear origin from the ligamentum nuchae, the spine of the vertebra prominens and from the spines of most of the thoracic vertebrae, together with the associated ligamenta supraspinalia.

The most cranial fibres run caudo-laterally to be attached to the lateral part of the shoulder girdle. The intermediate fibres are directed laterally and are inserted into the cranial border of the scapular spine. The caudal fibres pass cranially and become continuous with a short aponeurosis, most of which is inserted into a tubercle near the medial end of the caudal lip of the spine of the scapula.

Principal contrasts between locomotor groups: (Pls. 1-7) : In quadrupeds, the cranial part of m. trapezius is no thicker than the caudal region. The cranial fibres pass in a predominantly caudal direction and are inserted into the acromion and into the entire extent of the scapular spine which lies at right angles to the vertebral column.

In semibrachiators, the cranial part of the muscle is thicker than the caudal, and passes more laterally than in quadrupeds to insert into the lateral part of the clavicle, the acromion and much of the cranial edge of the more obliquely-placed scapular spine.

In brachiators, the cranial part of the muscle is even thicker relative to the caudal

region. Its fibres pass laterally and are inserted into the intermediate and lateral parts of the clavicle, the acromion, and lateral part of the obliquely-disposed scapular spine.

In man, as in quadrupeds, the cranial parts of m. trapezius are no thicker than the caudal, and pass inferiorly to insert into the acromion and the entire length of the horizontally-disposed spine. In contrast, however, some of the most superior fibres are attached to the lateral end of the clavicle.

Variation: (a) quadrupeds: (Pl. 1, fig. 3 and Pl. 2, fig. 7) : The cranial limit of origin of m. trapezius reached the external occipital protuberance, and a few fibres gained a fleshy attachment to the extreme medial end of the superior nuchal line. In the specimens of *Papio*, *Comopithecus* and *Mandrillus*, these fibres extended laterally on to the medial third of that line. The origin, while mostly fleshy, was interrupted between the lower part of the ligamentum nuchae and the third or fourth thoracic spine by a triangular aponeurosis. The caudal limit of the muscle lay most frequently at the level of the ninth thoracic spine (Table 9).

The muscle was uniformly thin and its cranial fibres passed caudally to meet the scapular spine approximately at right angles. Together with the intermediate fibres, they gained a linear insertion into practically the entire length of the spine of the scapula. In most New World quadrupeds, the insertion extended no more ventrally except in *Cacajao*, where it included the acromion and the capsule of the acromioclavicular joint. Hill (1960) found in individual specimens of *Callicebus* and *Cebus*, a few of the most cranial fibres of m. trapezius gaining attachment to the lateral end of the clavicle. In most Old World quadrupeds, the extreme lateral fibres inserted into the medial border of the acromion, but in one of the five dissections of *Macaca*, they extended ventrally to be attached to the capsule of the acromioclavicular joint. In the individual specimens of *Cynopithecus*, *Mandrillus* and *Cercopithecus* described by Patterson (1942), Pagenstecher (1867) and Dobson (1881), and in nine specimens of *Papio*, twenty-two of *Macaca* and twenty-two of *Cercopithecus* described by Dzwonkowski (1935), a few of the most cranial fibres of m. trapezius were inserted into the extreme lateral end of the clavicle.

In addition to their insertion into the tubercle on the scapular spine, the caudal fibres were attached to the medial quarter of its caudal lip.

(b) semibrachiators: (Pl. 3, fig. 11 and Pl. 4, fig. 15) : In the specimen of *Alouatta* the origin of m. trapezius included the whole of the superior nuchal line. In both specimens of *Colobus*, fibres arose from only the medial one third of this line while in the dissection of *Lagothrix*, the origin included the external occipital protuberance, but no part of the superior nuchal line. In *Ateles*, the cranial limit of origin lay on the ligamentum nuchae at the level of the spine of the axis.

The origin of m. trapezius was fleshy throughout, but Robertson (1944) found a small triangular aponeurosis in the lower cervical region of a specimen of *Lagothrix*.

The caudal limit of origin varied between the eighth and ninth thoracic spines (Table 9).

The cranial parts of the muscle were constantly thicker than its intermediate and caudal regions. The cranial fibres passed latero-ventrally to be attached to the

clavicle, the capsule of the acromioclavicular joint, the acromion and the lateral parts of the scapular spine. In *Alouatta*, *Ateles* and *Lagothrix*, the most lateral fibres were inserted into the lateral half of the clavicle; in the two specimens of *Colobus* and in one of *Lagothrix* (Robertson 1944), into the lateral third of the bone, and in a specimen of *Rhinopithecus* (Patterson 1942), into its lateral quarter.

A clavicular insertion has also been reported in an additional specimen of *Colobus* (Polak 1908) and in specimens of *Semnopithecus* (= *Presbytis*) *maurus* and *Semnopithecus nasicus* (= *Nasalis lavatus*) (Kohlbrugge 1897).

The intermediate fibres of m. trapezius passed almost horizontally to be inserted into the intermediate region of the spine of the scapula. The caudal fibres were inserted into a prominent tubercle on the spine, approximately a quarter of the way between the medial border of the scapula and the acromion, and marking the medial limit of the entire insertion.

(c) *brachiators*: (Pl. 5, fig. 19 and Pl. 6, fig. 23): In the specimens of *Gorilla* described by Hepburn (1892) and Stewart (1936), the origin of the most cranial fibres of m. trapezius extended over the medial two-thirds of the superior nuchal line, but in the instance figured by Raven (1950), the origin was restricted to the medial third. In our specimen of *Pongo*, these fibres covered the medial half of the superior nuchal line, while in that described by Hepburn (1892), the origin extended as far as the lateral end of the superior nuchal line. In *Pan*, the occipital attachment was restricted to the external protuberance; in *Hylobates* and *Symphalangus*, the cranial limit was the middle of the ligamentum nuchae.

The origin of m. trapezius was, throughout its length, fleshy, but Gratiolet and Alix (1866) and Miller (1952) described specimens of *Pan* in which there was a small triangular aponeurosis. The caudal limit varied as indicated in Table 9.

The fibres from the prominent cranial part of the muscle passed almost directly laterally and inserted into the lateral part of the clavicle, the acromion and the lateral part of the scapular spine. The clavicular insertion extended over the lateral two-thirds of the bone in *Hylobates*, *Symphalangus* and *Pan*, but in *Pongo* over the lateral third only as in all four specimens of *Gorilla* described by Hepburn (1892), Stewart (1936) and Raven (1950). The intermediate fibres passed laterally to be attached to the spine of the scapula medial to the insertion of the more cranial fibres. They did not extend medial to a prominent tubercle which lay close to the mid-point of the spine, and which received the tendinous insertion of the cranially-directed fibres of the caudal part of the muscle.

(d) *man*: (Pl. 7, fig. 27): The uppermost fibres of m. trapezius were attached to the medial third of the superior nuchal line, while the caudal limit of origin lay at the level of the twelfth thoracic segment (Table 9).

Between the vertebra prominens and the fourth thoracic vertebra, there was a triangular aponeurosis.

The most superior fibres passed infero-laterally, and the intermediate ones more horizontally, to gain a continuous insertion into the lateral third of the clavicle, the acromion and almost the entire length of the horizontally-disposed scapular spine. Most of the inferior fibres inserted into a tubercle on the spine of the scapula which was somewhat lateral to the extreme medial limit of insertion.

TABLE 9
Variation in the origin of m. trapezius (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from								
	Present study	Literature*	T.6	T.7	T.8	T.9	T.10	T.11	T.12	T.13 (= L.1)	T.14 (= L.2)
Quadrupeds ..	27	66	2.2	—	5.4	19.3	48.4	24.7	—	—	—
Semibrachiators	5	5	—	—	60.0	30.0	10.0	—	—	—	—
Brachiators ..	6	36	—	4.8	9.5	19.0	23.8	16.7	21.4	4.8	—
Man ..	3	80	—	—	2.4	2.4	18.1	27.7	42.2	6.0	1.2

Significance of differences in mean caudal limit of origin of m. trapezius : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P < 0.001$; Man and Semibrachiators : $P < 0.001$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P < 0.001$; Brachiators and Quadrupeds : $P = 0.2-0.1$; Semibrachiators and Quadrupeds : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which segments were spanned								
	Present study	Literature*	12	13	14	15	16	17	18	19	20
Quadrupeds ..	27	13	—	5.0	2.5	10.0	45.0	27.5	10.0	—	—
Semibrachiators	5	5	—	10.0	—	50.0	30.0	10.0	—	—	—
Brachiators ..	6	21	7.4	7.4	11.1	7.4	22.2	14.8	7.4	14.8	7.4
Man	3	—	—	—	—	—	—	—	—	100.0	—

Significance of differences in mean numbers of segments spanned by m. trapezius : Man, Brachiators, Semibrachiators and Quadrupeds : $P = 0.05-0.01$; Man and Brachiators : $P < 0.001$; Man and Semibrachiators : $P < 0.001$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P = 0.2-0.1$; Brachiators and Quadrupeds : $P > 0.9$; Semibrachiators and Quadrupeds : $P = 0.05-0.02$.

* Barnard 1875 ; Beaton & Anson 1942 ; Beattie 1927 ; Campbell 1937 ; Church 1861 ; Duvernoy 1855 ; Dzwonkowski 1935 ; Gratiolet & Alix 1866 ; Kallner 1956 ; Kohlbrugge 1897 ; Miller 1952 ; Patterson 1942 ; Pira 1913 ; Polak 1908 ; Primrose 1899 ; Raven 1950 ; Schuck 1913 ; Sommer 1907 ; Sonntag 1922 ; Stewart 1936 ; Sullivan & Osgood 1927.

M. atlantoscapularis anterior

General description: *M. atlantoscapularis anterior* is a thin, strap-like muscle that arises from the lateral mass of the atlas. Its fibres pass caudo-laterally to be inserted laterally on the shoulder girdle.

Principal contrasts between locomotor groups: (Pls. 1-7) : In quadrupeds, *m. atlantoscapularis anterior* passes mainly caudally to be inserted into the acromion and the lateral end of the spine of the scapula.

In semibrachiators, the fibres are more oblique, and their insertion is principally into the lateral end of the clavicle.

In brachiators, the fibres pass mainly laterally and are inserted laterally on the clavicle.

In man, *m. atlantoscapularis anterior* is usually absent.

Variation: (a) quadrupeds: (Pl. 1, fig. 3 and Pl. 2, fig. 8): The origin of m. atlantoscapularis anterior showed no noteworthy variation, and its direction was predominantly caudal. In *Aotes*, *Cacajao* and *Pithecia*, the muscle lay deep to the most cranial part of m. trapezius, as in all five specimens of *Cebus* described by Schuck (1913) and Campbell (1937) and in two of *Saimiri* (Campbell 1937). But in the remaining New World quadrupeds, m. atlantoscapularis anterior lay superficial to m. trapezius. In all Old World quadrupeds, it lay deep.

The muscle inserted mainly into the medial border of the acromion, but a few fibres were attached to the extreme lateral end of the scapular spine. In *Macaca*, *Papio*, *Comopithecus* and *Mandrillus*, fibres were attached to approximately the lateral half of this spine. In six specimens of *Macaca*, *Papio* and *Cercopithecus* (Schuck 1913) and in a specimen of *Cynopithecus* (Patterson 1942), the insertion extended over much of the lateral part of the spine of the scapula. In *Aotes*, *Cacajao*, and *Pithecia*, all fibres were inserted into the extreme lateral end of the spine.

Dobson (1881) reported in *Cercopithecus* an exceptional insertion of some fibres on to the lateral end of the clavicle.

(b) semibrachiators: (Pl. 3, figs. 9 and 11 and Pl. 4, fig. 16): From its origin on the lateral mass of the atlas, m. atlantoscapularis anterior was directed more laterally than in quadrupeds. In our specimens of *Alouatta* and *Lagothrix* and in one of *Ateles* described by Schuck (1913), the muscle lay superficial to m. trapezius, but in our specimens of *Ateles* and *Colobus* it lay deep.

In all available semibrachiators and in a specimen of *Semnopithecus nasicus* (= *Nasalis lavatus*) (Kohlbrugge 1897), m. atlantoscapularis anterior was inserted into the clavicle level with the insertion of the most cranial fibres of m. trapezius.

In one specimen of *Colobus* (Polak 1908), and in a specimen of *Rhinopithecus* (Patterson 1942), the muscle inserted into both the acromion and the lateral end of the clavicle. In our specimen of *Alouatta*, in a further example of this genus (Campbell 1937), and in two of *Ateles* (Schuck 1913; Campbell 1937) the muscle inserted by two heads. The more cranial of these was attached to the middle of the clavicle, and the more caudal to the lateral end of the spine and acromion. Kohlbrugge (1897) described a specimen of *Semnopithecus* (= *Presbytis*) *maurus* where in contrast to other semibrachiators, the insertion was restricted to the acromion.

(c) brachiators: (Pl. 5, fig. 18 and Pl. 6, fig. 24): In the available brachiators and in two specimens of *Gorilla* described by Raven (1950), the origin of m. atlantoscapularis anterior showed no noteworthy variations. Stewart (1936) described a specimen of *Pongo* in which fibres took additional origin from the transverse process of the axis, while Owen (1830) reported on another individual where some fibres were attached to the occiput.

M. atlantoscapularis anterior passed even more laterally than in semibrachiators and consistently lay deep to m. trapezius. But in a specimen of *Pan* (Champneys 1872), the muscle lay superficially.

In all cases, the muscle was inserted into the clavicle level with the most cranial fibres of m. trapezius. In one of the two gorillas described by Raven (1950) some

fibres of m. atlantoscaphularis anterior were attached to the tendon of m. subclavius, while in three specimens of *Hylobates* described by Schuck (1913), some fibres gained attachment to the ligamentum cleidoangulare.

Barnard (1875) reported the absence of m. atlantoscaphularis anterior in a specimen of *Pongo*.

(d) *man*: M. atlantoscaphularis anterior was absent in the three subjects dissected, but Parsons (1898) and Walmsley (1918) have described subjects in which it occurred, taking origin from the lateral mass of the atlas, passing obliquely and deep to m. trapezius, to be inserted into the clavicle between its intermediate and lateral thirds. Brown (1880) described another case in which some fibres of m. atlantoscaphularis anterior arose from the transverse process of the axis. In yet another example (Beaton & Anson 1942), the muscle fused distally with the deep surface of m. trapezius.

M. serratus magnus (vel anterior) pars caudalis

General description: This division of m. serratus magnus (vel anterior) is fan-shaped, comprising a number of fleshy bundles arising from the lateral surface of the thoracic cage and separated from the pars cranialis by loose areolar tissue. Near their origin the fasciculi are separate, but they converge upon a semilunar tendon which is inserted into the inferior angle of the scapula and into the adjacent part of its medial border.

Principal contrasts between locomotor groups (Pls. 1-7 and Table 10) : In quadrupeds, m. serratus magnus pars caudalis comprises, on average, six muscular slips whose length and thickness do not differ markedly from the fasciculi comprising the pars cranialis.

In semibrachiators, the number of digitations is increased on average to eight or nine, and these are both longer and thicker than in the pars cranialis.

In brachiators, there are usually nine or ten digitations, and each is, relative to the fasciculi comprising the pars cranialis, thicker and longer than in any other locomotor group.

In man, there are no more digitations than in quadrupedal monkeys, but in contrast, each fasciculus is somewhat thicker and longer than in the pars cranialis.

Variation: (a) *quadrupeds*: (Pl. 1, fig. 4 and Pl. 2, fig. 8) : M. serratus magnus pars caudalis usually comprised six fasciculi taking origin from the fourth to ninth ribs (Table 10), and inserting as in the Anthroidea as a whole.

(b) *semibrachiators*: (Pl. 3, fig. 12 and Pl. 4, fig. 16) : M. serratus magnus pars caudalis comprised nine or ten digitations (Table 10). No noteworthy variations were encountered in the pattern of insertion.

In a specimen of *Colobus*, Polak (1908) noted the strong development of this part of m. serratus magnus.

(c) *brachiators*: (Pl. 5, fig. 20 and Pl. 6, fig. 24) : M. serratus anterior pars caudalis comprised eight to eleven digitations (Table 10). No variations in the method of insertion were observed.

TABLE 10

Variation in the origin of *m. serratus magnus* (vel anterior) pars caudalis (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from ribs						
	Present study	Literature*	1	2	3	4	5	6	7
Quadrupeds ..	26	74	—	—	5.0	24.0	69.0	—	2.0
Semibrachiators	5	5	—	50.0	50.0	—	—	—	—
Brachiators ..	6	20	3.9	11.5	73.1	11.5	—	—	—
Man	3	0	—	—	—	100.0	—	—	—

Significance of differences in mean cranial limit of origin of *m. serratus magnus* pars caudalis : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P < 0.001$; Man and Semibrachiators : $P < 0.001$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P \approx 0.05$; Brachiators and Quadrupeds : $P < 0.001$; Semibrachiators and Quadrupeds : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs					
	Present study	Literature*	8	9	10	11	12	13
Quadrupeds ..	26	78	22.1	46.2	28.8	1.0	1.9	—
Semibrachiators	5	5	10.0	20.0	40.0	—	10.0	20.0
Brachiators ..	6	33	—	—	28.2	33.3	15.4	23.1
Man	3	0	100.0	—	—	—	—	—

Significance of differences in mean caudal limit of origin of *m. serratus magnus* pars caudalis : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P < 0.001$; Man and Semibrachiators : $P = 0.01-0.001$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P \approx 0.2-0.1$; Brachiators and Quadrupeds : $P < 0.001$; Semibrachiators and Quadrupeds : $P = 0.05-0.02$.

Locomotor group	Number of specimens		Percentage of cases in which ribs were spanned							
	Present study	Literature*	4	5	6	7	8	9	10	11
Quadrupeds ..	26	74	14.0	29.0	56.0	1.0	—	—	—	—
Semibrachiators	5	5	—	—	—	10.0	40.0	20.0	10.0	20.0
Brachiators ..	6	20	—	—	—	—	15.4	34.6	30.8	19.2
Man	3	0	—	100.0	—	—	—	—	—	—

Significance of differences in mean numbers of ribs spanned by *m. serratus magnus* pars caudalis : Man, Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Man and Brachiators : $P < 0.001$; Man and Semibrachiators : $P < 0.001$; Man and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P = 0.2-0.1$; Brachiators and Quadrupeds : $P < 0.001$; Semibrachiators and Quadrupeds : $P < 0.001$.

* Beattie 1927 ; Bischoff 1880 ; Broca 1869 ; Champneys 1872 ; Gratiolet & Alix 1866 ; Hepburn 1892 ; Kallner 1956 ; Kohlbrugge 1897 ; Matsuo 1960 ; Miller 1952 ; Pagenstecher 1867 ; Patterson 1942 ; Pira 1913 ; Polak 1908 ; Primrose 1899 ; Raven 1950 ; Schuck 1913 ; Sommer 1907 ; Sonntag 1922 ; Stewart 1936 ; Sullivan & Osgood 1927 ; Wilder 1863.

(d) *man*: (Pl. 7, fig. 28) : *M. serratus anterior pars caudalis* comprised five digitations arising from the fourth to eighth ribs. Standard texts indicate that in some cases the number may be reduced to four. The insertion of the muscle agreed with that common to monkeys and apes.

Muscles responsible for stabilizing the shoulder joint

M. supraspinatus

General description: *M. supraspinatus* is wedge-like and pennate, its fibres taking origin from the medial two-thirds of the supraspinous fossa and, in the region of the suprascapular notch, from the fascia covering *m. subscapularis*. The fibres converge upon a short, stout tendon which adheres to the capsule of the shoulder joint and is inserted into the most proximal part of the greater tuberosity.

Principal contrasts between locomotor groups: (Pls. 1-7) : No features of this muscle were found to afford any contrast between different locomotor groups.

Variation: (a) *quadrupeds*: (Pl. 1, fig. 4 and Pl. 2, fig. 8) : In all specimens of this group, the muscle was long and narrow compared with *m. infraspinatus*.

(b) *semibrachiators*: (Pl. 3, fig. 12 and Pl. 4, fig. 16) : While in our specimens of *Colobus*, *m. supraspinatus* was, as in quadrupeds, long and narrow, in *Alouatta*, *Ateles* and *Lagothrix*, the muscle was broad and short. This was also noted for the seven specimens of these genera described by Campbell (1937).

(c) *brachiators*: (Pl. 5, fig. 20 and Pl. 6, fig. 24) : In *Pongo*, the proportions of *m. supraspinatus* were similar to those seen in quadrupeds. In *Hylobates*, *Symphalangus* and *Pan*, and in *Gorilla* (Raven 1950) the muscle was relatively broader.

(d) *man*: (Pl. 7, fig. 28) : In man, *m. supraspinatus* was, as in quadrupeds, relatively long and narrow.

Mm. infraspinatus et teres minor

General description: *Mm. infraspinatus et teres minor* are triangular and pennate, taking origin from the medial two-thirds of the infraspinous fossa, from the intermediate part of the lateral border of the scapula and from the caudal surface of its spine. Many fibres also arise from the fascia investing the muscle.

The fibres arising from the lateral border of the scapula, and which, in man, form a separate muscle (*m. teres minor*), converge upon a short stout tendon which adheres to the dorsal aspect of the capsule of the shoulder joint and inserts distally into the greater tuberosity. But the bulk of the fibres converge on to a stout, rectangular tendon, whose proximal part lies deep to the fleshy fibres. This tendon passes freely over the dorsal aspect of the joint-capsule and is inserted into the greater tuberosity distal to the attachment of *m. supraspinatus*.

Principal contrasts between locomotor groups: (Pls. 1-7) : No features of the muscle appeared to vary in relation to locomotor groupings.

Variation: (a and b) quadrupeds and semibrachiators: (Pl. 1, fig. 4; Pl. 2, fig. 8; Pl. 3, fig. 12 and Pl. 4, fig. 16) : In these groups, the fibres arising from the lateral margin of the scapula were fused proximally with the rest of the muscle.

(c) *brachiators:* (Pl. 5, fig. 20 and Pl. 6, fig. 24) : In *Hylobates* and *Symphalangus*, the most lateral fibres were, as in quadrupeds and semibrachiators, fused with the main part of the muscle. In *Pan* and *Pongo*, and in the three specimens of *Gorilla* described by Hepburn (1892) and Raven (1950) this part was bigger and was clearly separated from the remainder of the muscle to form a separate unit—m. teres minor.

(d) *man:* (Pl. 7, fig. 28) : The fibres comprising m. teres minor were, as in the great apes, clearly separated from m. infraspinatus.

M. subscapularis

General description: M. subscapularis is triangular and multipennate, taking origin from the subscapular fossa except around the scapular neck. The fibres converge upon a short, thick tendon which adheres to the medial part of the capsule of the shoulder joint and is inserted into the lesser tuberosity of the humerus.

Variation: No variations in this muscle were found either between the different locomotor groups, or between the individuals within each.

Muscles responsible for stabilizing the shoulder girdle

M. rhomboideus

General description: M. rhomboideus is a thin sheet taking origin from the ligamentum nuchae, the spines of the seventh cervical and upper thoracic vertebrae, and the associated ligamenta supraspinalia. The fibres pass caudo-laterally to be inserted dorsal to the fibres of m. serratus magnus (m. serratus anterior) into the entire length of the medial border of the scapula.

Principal contrasts between locomotor groups: (Pls. 1–7 and Table 11) : There appears to be no correlation between the four locomotor groups and the considerable variations in m. rhomboideus.

Variation: (a) quadrupeds: (Pl. 1, fig. 4 and Pl. 2, fig. 8) : The muscle had an occipital origin of variable extent. This sometimes formed a head, distinct from the rest of the muscle which was itself, in isolated instances, subdivided.

Variations in the caudal limit of origin of m. rhomboideus are listed in Table 11.

The occipital origin of m. rhomboideus included the medial third of the superior nuchal line, except in *Papio*, *Comopithecus* and *Mandrillus*, where it extended over the medial two-thirds.

In *Saimiri* and *Pithecia*, the occipital fibres were separated by a thin strip of loose areolar tissue from the remainder of the muscle. A similar division was

found by Campbell (1937) consistently in six specimens of *Aotes*, *Saimiri* and *Leontocebus*, and in two of three specimens of *Cebus*.

In *Callithrix*, Beattie (1927) found that the occipital head of m. rhomboideus was typically separated by an appreciable gap from the caudal part of the muscle, whose cranial fibres gained attachment to the ligamentum nuchae opposite the third cervical spine. An even bigger gap was found (a) in a specimen of *Cynopithecus* (Patterson 1942) where the cranial limit of the caudal part of the muscle was opposite the fourth cervical spine, (b) in two specimens of *Mandrillus* (Pagenstecher 1867), where the corresponding limit lay at the level of the fifth cervical spine and (c) in a further specimen of this genus (Sonntag 1924), where this limit was the seventh cervical spine.

In *Callithrix* (Beattie 1927) and in *Cynopithecus* (Patterson 1942), the caudal part of m. rhomboideus was also found to be divided.

The direction and insertion of the muscle fibres did not deviate from the pattern typical of the other groups of the Anthropeidea.

In four specimens of *Aotes* and *Leontocebus* (Campbell 1937) and in a single specimen of *Cercopithecus* (Mivart 1865), a fasciculus took origin from the lateral mass of the atlas and passed caudo-laterally to be attached to the superior angle of the scapula as a separate muscle—m. atlantoscapularis posterior.

(b) *semibrachiators*: (Pl. 3, fig. 12 and Pl. 4, fig. 16) : An occipital head was usually separated from the more caudal parts of the muscle, which arose from the ligamentum nuchae, the seventh cervical spine and the spines and ligamenta supraspinalia of the upper six or seven thoracic vertebrae (Table 11).

In all examples dissected in the present study and in eight specimens of *Alouatta*, *Ateles* and *Colobus* (Polak 1908 ; Schuck 1913 ; Campbell 1937), the occipital part of the origin included the external occipital protuberance and a small adjoining length of the superior nuchal line.

In the specimens of *Colobus*, the origin of m. rhomboideus was undivided. There was a narrow division in the muscle at the level of the external occipital protuberance in all six specimens of *Alouatta*, *Ateles* and *Lagothrix* (Campbell 1937). In our specimens of these genera, in a specimen of *Ateles* described by Schuck (1913) and in two of *Colobus* described by Polak (1908) the occipital head was separated from the caudal part of the muscle by a big gap. In a specimen of *Lagothrix* (Robertson 1944), two occipital heads were present.

In a specimen of *Colobus* (Polak 1908) and in one of *Lagothrix* (Robertson 1944), the caudal part of m. rhomboideus was divided opposite the seventh cervical spine.

The direction and pattern of insertion of the muscle showed no noteworthy variations.

In our specimen of *Alouatta*, a bundle of fibres arising from the lateral mass of the atlas formed a distinct m. atlantoscapularis posterior. This was also found by Campbell (1937) in one of four specimens of *Ateles*, and in one of two of *Lagothrix*, and by Robertson (1944) in each of three of this latter genus.

(c) *brachiators*: (Pl. 5, fig. 20 and Pl. 6, fig. 24) : In our specimens of *Hylobates*, *Symphalangus* and *Pan*, and in three of *Gorilla* described by Hepburn (1892), Stewart (1936) and Raven (1950), the most cranial fibres of m. rhomboideus arose

from the middle of the ligamentum nuchae, and the muscle comprised an uninterrupted sheet extending caudally as far as the fifth or sixth thoracic spine (Table 11). Champneys (1872), in a specimen of *Pan*, noted the division of m. rhomboideus by fibrous tissue into cranial and caudal parts.

In our specimen of *Pongo* and in three described by Sandifort (1841) and Michaelis (1903), the cranial limit of origin of the main part of the muscle was on the ligamentum nuchae. But in the present specimen, an additional small slip took origin from the external occipital protuberance and the adjacent part of the superior nuchal line. A separate occipital head of m. rhomboideus was also found in all five specimens of *Pongo* dissected by Hepburn (1892), Sullivan and Osgood (1927), Stewart (1936) and Kallner (1956). In the five specimens studied by Church (1861), Bischoff (1870), Hepburn (1892), Primrose (1899) and Schuck (1912), fibres took origin from the superior nuchal line but were not separated from those arising from the ligamentum nuchae.

TABLE 11
Variation in the origin of m. rhomboideus (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was at the level of					
	Present study	Literature*	T.3	T.4	T.5	T.6	T.7	T.8
Quadrupeds ..	27	21	8.3	33.3	25.0	25.0	8.3	—
Semibrachiators	5	15	—	5.0	25.0	20.0	40.0	10.0
Brachiators ..	6	27	9.1	18.2	12.1	30.3	30.3	—
Man	3	0	—	—	100.0	—	—	—

Significance of differences in mean caudal limit of origin of m. rhomboideus : Brachiators, Semibrachiators and Quadrupeds : $P < 0.001$; Brachiators and Semibrachiators : $P = 0.05-0.02$; Brachiators and Quadrupeds : $P = 0.05-0.02$; Semibrachiators and Quadrupeds : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which spines were spanned										
	Present study	Literature*	6	7	8	9	10	11	12	13	14	15	
Quadrupeds ..	27	21	2.1	—	4.2	2.1	—	8.3	33.3	16.7	25.0	8.3	
Semibrachiators	5	8	—	7.7	7.7	15.4	7.7	23.1	—	30.7	7.7	—	
Brachiators ..	6	26	6.3	6.3	15.6	3.1	9.3	18.8	12.5	9.3	12.5	6.3	
Man	3	0	—	—	—	100.0	—	—	—	—	—	—	

Significance of differences in mean numbers of vertebral spines spanned by m. rhomboideus : Brachiators, Semibrachiators and Quadrupeds : $P = 0.01-0.001$; Brachiators and Semibrachiators : $P = 0.9-0.8$; Brachiators and Quadrupeds : $P = 0.01-0.001$; Semibrachiators and Quadrupeds : $P = 0.05-0.02$.

* Beattie 1927 ; Bischoff 1870 ; Campbell 1937 ; Church 1861 ; Gratiolet & Alix 1866 ; Hepburn 1892 ; Kallner 1956 ; Kohlbrugge 1897 ; Michaelis 1903 ; Miller 1952 ; Pagenstecher 1867 ; Patterson 1942 ; Pira 1913 ; Polak 1908 ; Primrose 1899 ; Raven 1950 ; Robertson 1944 ; Sandifort 1841 ; Schuck 1913 ; Sommer 1907 ; Sonntag 1922, 1923 ; Stewart 1936 ; Sullivan & Osgood 1927.

In all brachiators, the direction and pattern of insertion of the complete muscle showed no noteworthy differences from the corresponding features in monkeys.

(d) *man*: (Pl. 7, fig. 28) : The origin of m. rhomboideus extended superiorly as far as the lower part of the ligamentum nuchae and inferiorly to the fifth thoracic spine. The muscle was divided between the seventh cervical and first thoracic vertebrae into a superior part (m. rhomboideus minor) and an inferior part (m. rhomboideus major).

The insertion of m. rhomboideus minor was continuous with that of m. rhomboideus major, the combined insertion not differing from the pattern common to monkeys and apes.

Variation in the insertion of mm. rhomboidei in a series of one hundred human subjects was investigated by Balli (1906). In fifty-four per cent of cases, the insertion did not differ from that described for m. rhomboideus in monkeys and apes. In twenty-one per cent of cases, m. rhomboideus major inserted into a ligamentous arch whose ends were attached to the medial border of the scapula near the base of the spine and near the inferior angle. In nineteen per cent of cases, the muscle inserted into a ligament attached near the inferior angle. In six per cent of cases, the muscle inserted into a ligament which presented the appearance of a double arch attached to the medial border of the scapula near the base of the spine, near the inferior angle and half way between the two.

Curnow (1873) described a subject in which a distinct m. atlantoscapularis posterior arose from the lateral mass of the atlas and inserted into the superior angle of the scapula.

M. serratus magnus pars cranialis (m. levator scapulae plus m. serratus anterior pars cranialis)

General description: The fibres of m. serratus magnus pars cranialis (m. levator scapulae plus m. serratus anterior pars cranialis) take origin from certain cervical transverse processes and as a series of digitations from the upper ribs. The fibres pass caudo-dorsally. The cervical slips are inserted around the superior angle of the scapula, while the remainder gain attachment to the medial border except near the inferior angle.

Principal contrasts between locomotor groups: Such variations as were noted in the features of this muscle did not appear to correlate with the locomotor groups used in this study.

Variation: (a and b) quadrupeds and semibrachiators: (Pl. 1, fig. 4 ; Pl. 2, fig. 8 ; Pl. 3, fig. 12 and Pl. 4, fig. 16) : Variations in the extent of origin of m. serratus magnus pars cranialis are summarized in Table 12. In all specimens of the Ceboidea, the cervical fibres formed a muscular sheet, separated by a thin septum of areolar tissue from the digitation arising from the first rib. In most specimens of the Cercopithecoidea, the fasciculi arising from adjacent cervical transverse processes were discrete. But in one specimen of *Macaca* a single separation only occurred between the fifth and sixth cervical vertebrae. In those of *Papio* and *Comopithecus*, a similar septum lay between the third and fourth vertebrae.

Beattie (1927) found that in *Callithrix*, muscular fasciculi were typically absent from the lower cervical region, there thus being a conspicuous triangular gap between the cervical and costal digitations. A corresponding separation was found in all five specimens of *Ateles*, *Macaca*, *Mandrillus* and *Colobus* described by Schuck (1913), Duvernoy (1855), Sonntag (1922) and Polak (1908).

(*c and d*) *brachiators and man*: (Pl. 5, fig. 20; Pl. 6, fig. 24 and Pl. 7, fig. 28): Variations in the extent of origin of m. levator scapulae plus m. serratus anterior pars cranialis in these groups are summarized in Table 12.

Cervical fibres arose from only the most cranial transverse processes and formed a separate unit—m. levator scapulae, separated by a prominent triangular space from the costal digitations of m. serratus anterior. Fibre-bundles of m. levator scapulae from adjacent cervical transverse processes were, in turn, partly separated from each other by areolar septa. In the two specimens of *Pongo* described by Duvernoy (1855) and Hepburn (1892), the cranial fibres of m. levator scapulae comprised a small distinct bundle arising from the mastoid process.

The general direction and insertion of the fibres were similar to the corresponding features of monkeys, m. levator scapulae inserting around the superior angle of the scapula and m. serratus anterior pars cranialis into the medial margin except near the inferior angle.

TABLE 12

Number of segments spanned by m. serratus magnus pars cranialis (Anthropoidea).

Locomotor group	Number of specimens		Percentage of cases in which				
	Present study	Literature*	7	8	9	10	11
Quadrupeds ..	27	22	2.0	32.7	24.5	38.8	2.0
Semibrachiators	5	4	—	55.6	44.4	—	—
Brachiators ..	6	16	—	18.2	68.2	13.6	—
Man	3	0	—	—	—	100.0	—

Significance of differences in mean numbers of segments spanned by m. serratus magnus pars cranialis: Man, Brachiators, Semibrachiators and Quadrupeds: $P=0.05-0.01$; Man and Brachiators: $P<0.001$; Man and Semibrachiators: $P<0.001$; Man and Quadrupeds: $P<0.001$; Brachiators and Semibrachiators: $P=0.05-0.02$; Brachiators and Quadrupeds: $P=0.6-0.5$; Semibrachiators and Quadrupeds: $P=0.01-0.001$.

* Beattie 1927; Broca 1869; Champneys 1872; Church 1861; Deniker 1885; Duvernoy 1855; Fick 1895; Gratiolet & Alix 1866; Hepburn 1892; Kallner 1956; Kohlbrugge 1897; Macalister 1873; Miller 1952; Pagenstecher 1867; Patterson 1942; Petelska 1953; Pira 1913; Polak 1908; Primrose 1899; Raven 1950; Schuck 1913; Sommer 1907; Sonntag 1922, 1923; Stewart 1936; Sullivan & Osgood 1927; Sutton 1883; Wilder 1863.

M. subclavius

General description: *M. subclavius* is small and triangular, arising by a short tendon from the cranial border of the first rib close to the costo-chondral junction. Its fibres pass cranio-laterally to gain a fleshy insertion into the caudal aspect of the clavicle.

The dorsal and ventral surfaces of the muscle are covered by fascial sheets which are attached cranially to the clavicle and which fuse caudally to blend with the fascia clavipectoralis.

Principal contrasts between locomotor groups: (Pls. 1-7) : In quadrupedal monkeys, m. subclavius is inserted into the intermediate third of the clavicle.

In semibrachiators and brachiators, the clavicular insertion extends more laterally and some fibres are also attached to the ligamentum coracoclaviculare. The fascia clavipectoralis is thickened and forms a prominent ligamentum costocoracoideum, more developed in brachiators than in semibrachiators.

In man, the insertion of m. subclavius is, as in quadrupeds, restricted to the intermediate region of the clavicle, and there is little thickening of the fascia clavipectoralis.

Variation: (a) *quadrupeds:* (Pl. 1, fig. 2 and Pl. 2, fig. 6) : No noteworthy variations in m. subclavius were recorded in any of the quadrupedal monkeys studied.

(b) *semibrachiators:* (Pl. 3, fig. 10 and Pl. 4, fig. 14) : The insertion of m. subclavius extended over the lateral third of the clavicle and in *Alouatta*, *Ateles* and *Lagothrix* included the ligamentum coracoclaviculare and the adjoining part of the coracoid process. In two specimens of *Colobus* described by Polak (1908), the insertion was into the lateral half of the clavicle and in a specimen of *Rhinopithecus* described by Patterson (1942) into the lateral three-fifths.

The fascia clavipectoralis was thickened on the ventral aspect of m. subclavius to form a prominent ligamentum costocoracoideum attached laterally to the tip of the coracoid process. In our specimens of *Ateles* and *Lagothrix*, its medial end was attached to the first rib, while in those of *Colobus* and *Alouatta* and in two specimens of *Alouatta* described by Campbell (1937), the medial limit of attachment was to the medial part of the clavicle.

(c) *brachiators:* (Pl. 5, fig. 18 and Pl. 6, fig. 22) : In this group including the specimens of *Gorilla* described by Raven (1950), Stewart (1936) and Hepburn (1892), m. subclavius took origin from the first costochondral junction. In a specimen of *Hylobates* (Stewart 1936) and in one of *Pongo* (Hepburn 1892), it also arose from the second costal cartilage. In two other specimens of *Hylobates* (Hepburn 1892 ; Kohlbrugge 1897), the origin extended still further to include both the second and third costal cartilages.

In this group, m. subclavius inserted constantly into the lateral part of the clavicle.

Duvernoy (1855) recorded the absence of m. subclavius in a specimen of *Gorilla*.

In the specimens of *Gorilla* figured by Raven (1950), the thickened fascia clavipectoralis (ligamentum costocoracoideum) appeared relatively stronger than in the specimens of *Hylobates*, *Symphalangus* and *Pan* examined in the present study. In our dissection of *Pongo*, the ligament was not only exceptionally strong but was also chondrified.

(d) *man:* (Pl. 7, fig. 26) : The origin and direction of fibres of m. subclavius did not differ from the pattern general to the Anthropoidea. Its insertion was into a fossa on the inferior surface of the intermediate region of the clavicle.

M. omohyoideus

General description: *M. omohyoideus* is small and ribbon-like, arising from the extreme ventro-lateral aspect of the hyoid bone. Its fibres pass dorso-laterally to be inserted into the superior border of the scapula.

Principal contrasts between locomotor groups: The few variations of this muscle appear unrelated to differences in modes of locomotion.

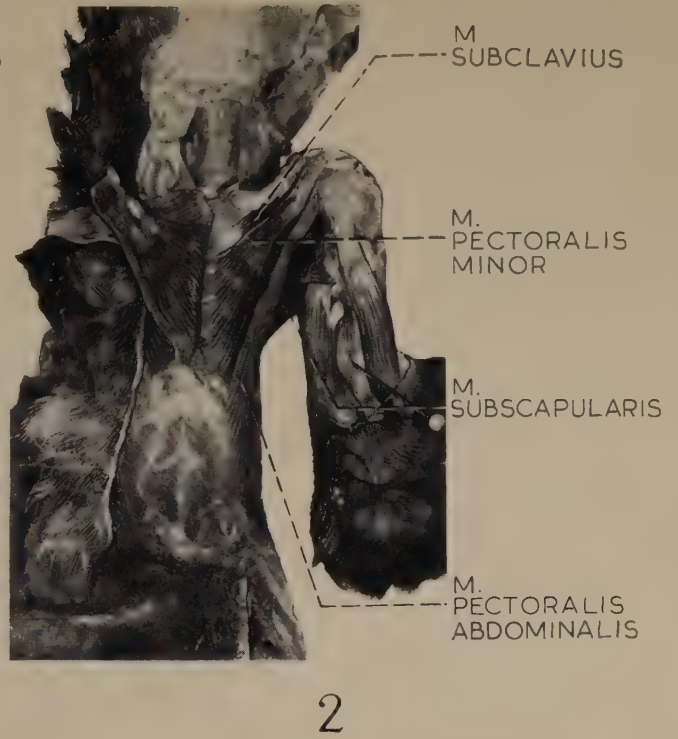
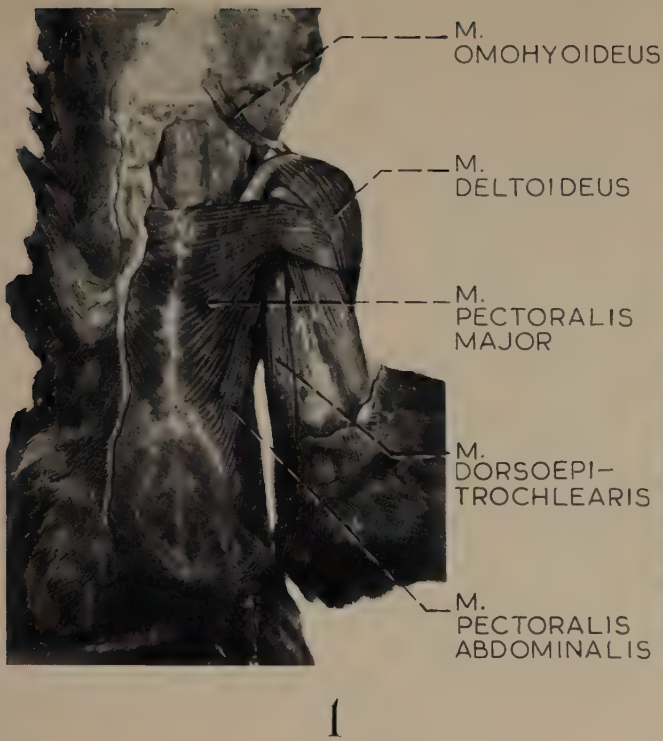
Variation: (a and b) quadrupeds and semibrachiators: (Pl. 1, fig. 1 and Pl. 4, fig. 14) : In our specimens of the Ceboidea and Cercopithecoidea, *m. omohyoideus* was straplike, passing deep to *m. sternocleidomastoideus*. In the Cercopithecoidea, it inserted into the intermediate part of the superior border of the scapula. In most of the Ceboidea, the insertion was into the lateral end of this border but in *Pithecia* and *Cacajao*, into the medial end. *M. omohyoideus* was absent in our specimens of *Ateles* and *Lagothrix*, in ten specimens of *Aotes*, *Alouatta*, *Ateles* and *Lagothrix* (Campbell 1937, Parsons 1898) and in single specimens of *Semnopithecus* (= *Presbytis*) *maurus* and *Semnopithecus nasicus* (= *Nasalis lavatus*) (Kohlbrugge 1897).

(c and d) brachiators and man: (Pl. 5, fig. 17 and Pl. 6, fig. 21) : In our specimens of *Hylobates* and *Symphalangus*, *m. omohyoideus* was straplike, but in the great apes and man, it comprised two bellies joined by an intermediate tendon. The absence of an intermediate tendon has been reported in *Pongo* (Bischoff 1870 ; Sonntag 1924), in *Pan* (Sonntag 1924) and in man (Gegenbaur 1876 ; Walmsley 1918). In a specimen of *Pan*, described by Sonntag (1923), *m. omohyoideus* comprised three radiating bellies while Raven (1950) in a specimen of *Gorilla*, found three bellies in series. In our specimens of *Hylobates*, *Symphalangus* and *Pan*, the muscle inserted into the intermediate region of the superior border of the scapula. In *Pongo*, in *Gorilla* as figured by Raven (1950) and in man, the insertion was into the lateral edge of the scapular notch.

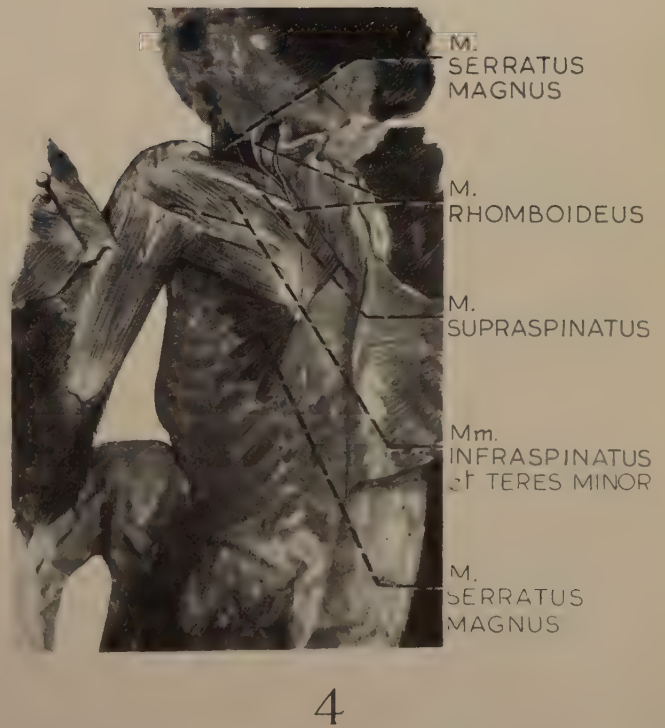
PLATE 1

PLATE 1

Figs. 1-4 The shoulder muscles of a quadrupedal New World monkey—*Aotes sp.*



5 CENTIMETRES

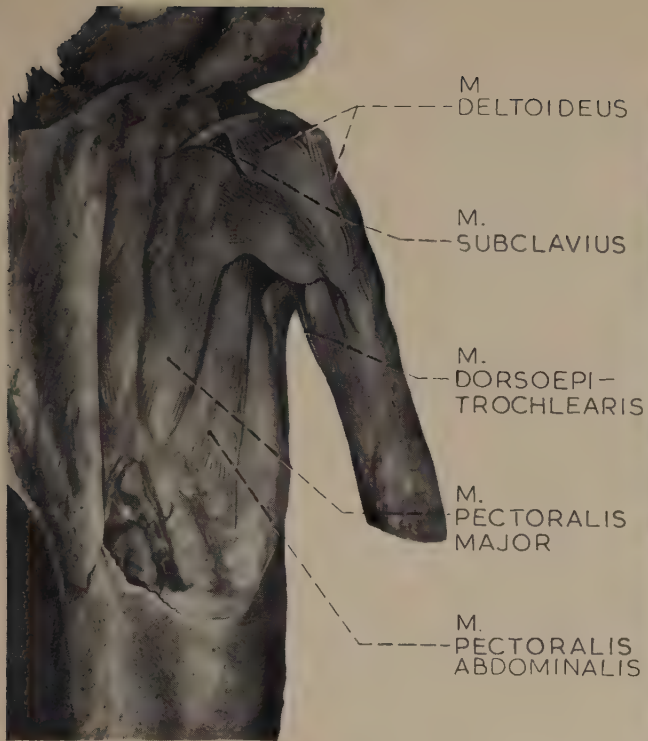


Figs. 1-4. The shoulder muscles of a quadrupedal New World monkey—*Aotes* sp.

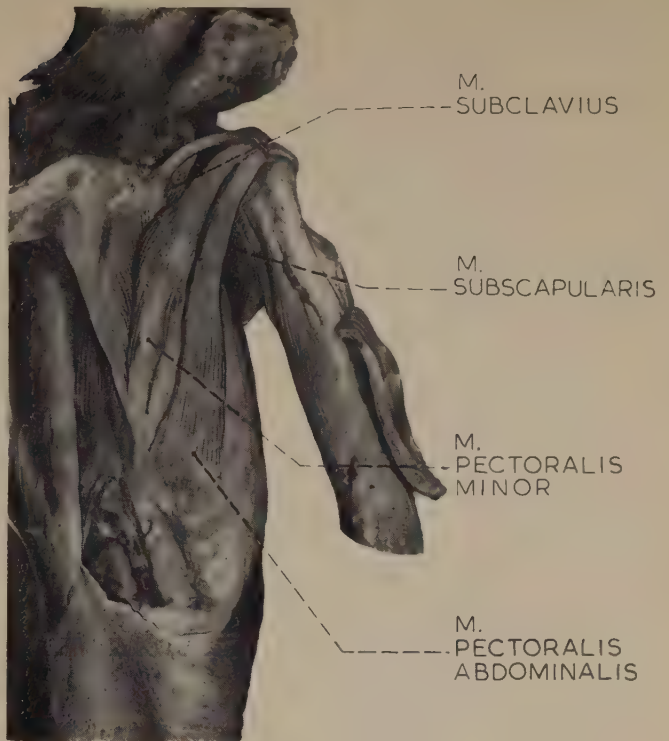
PLATE 2

PLATE 2

Figs. 5-8 The shoulder muscles of a quadrupedal Old World monkey—*Mandrillus sp.*



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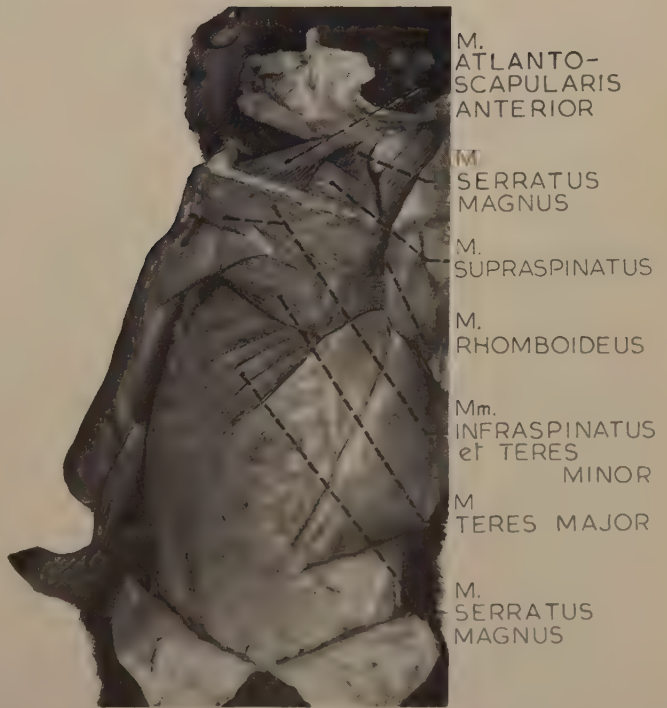


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5 CENTIMETRES



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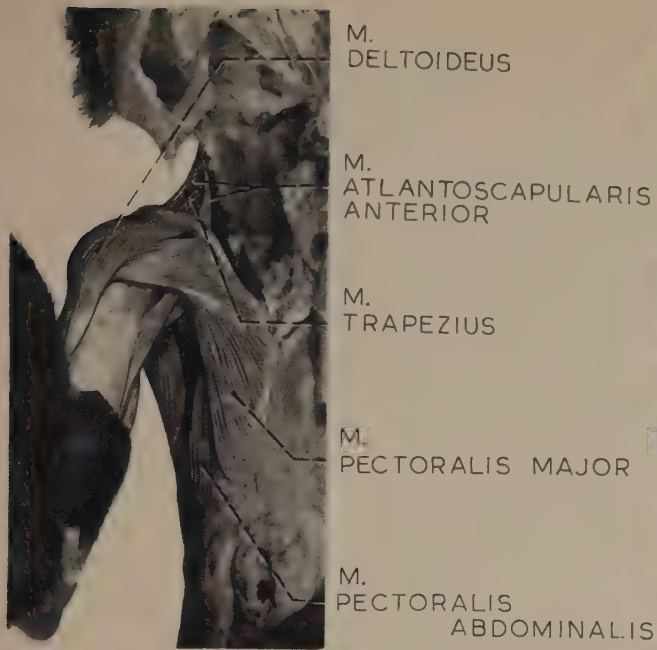
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Figs. 5-8. The shoulder muscles of a quadrupedal Old World monkey—*Mandrillus* sp.

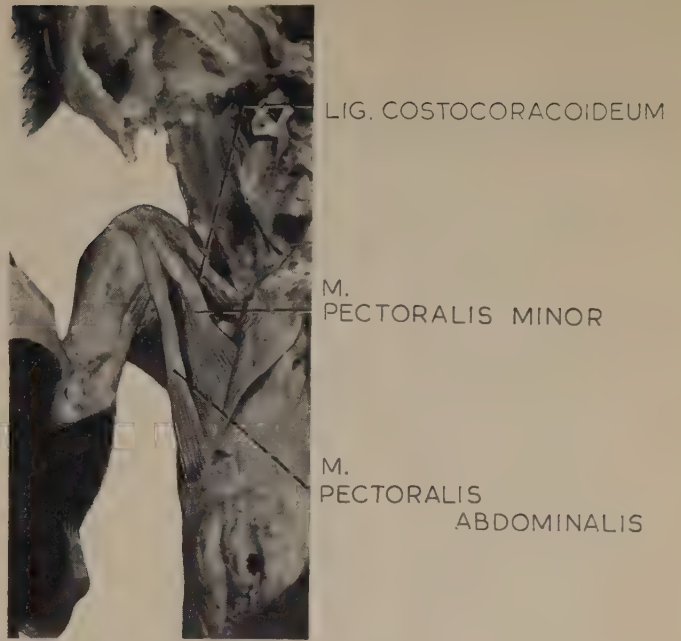
PLATE 3

PLATE 3

Figs. 9-12 The shoulder muscles of a New World semibrachiator—*Alouatta sp.*

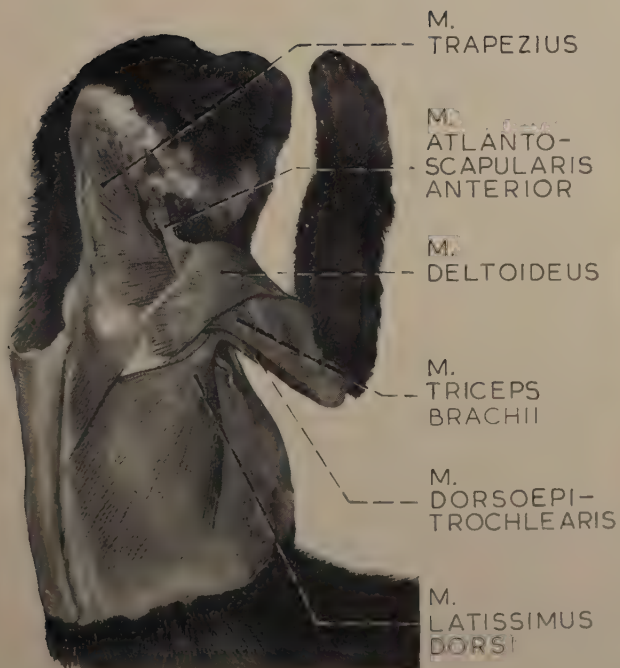


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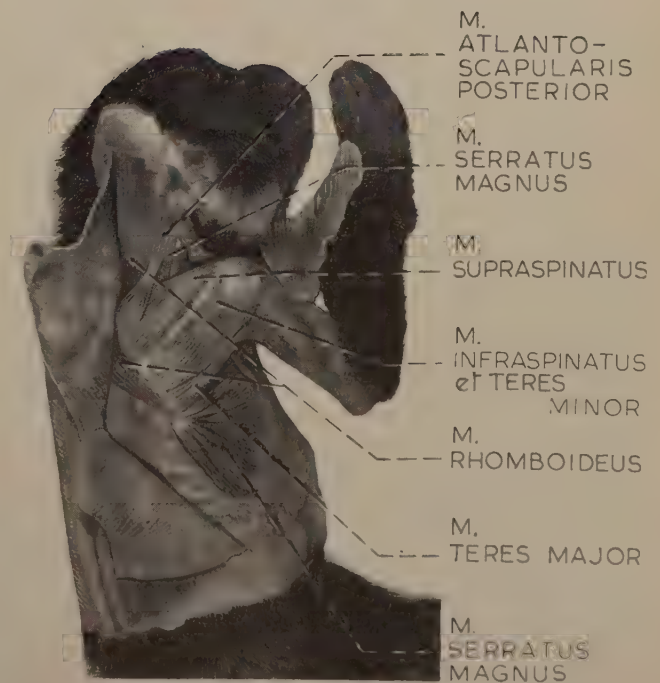


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5 CENTIMETRES



11



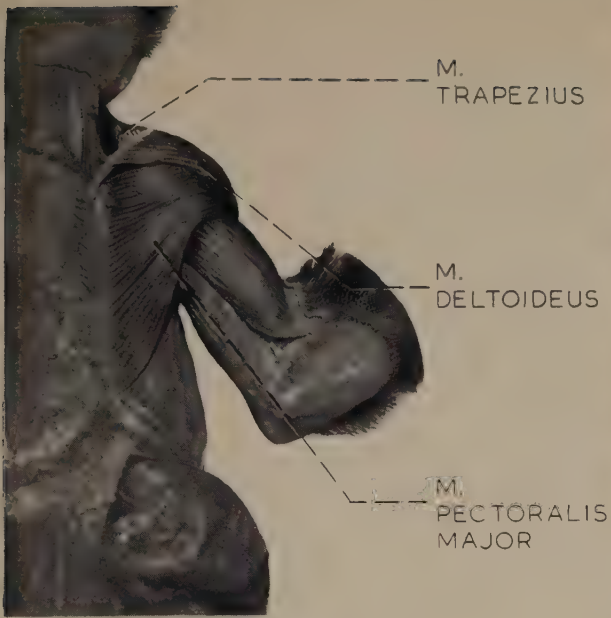
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Figs. 9-12. The shoulder muscles of a New World semibrachiator—*Alouatta* sp.

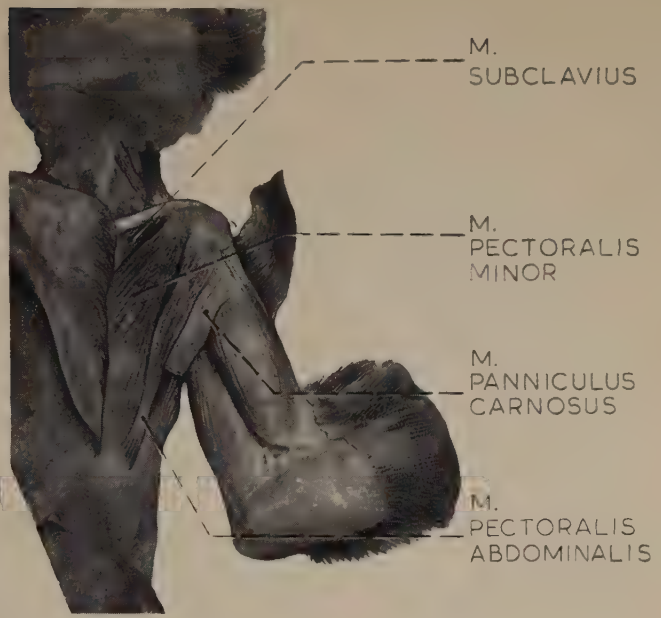
PLATE 4

PLATE 4

Figs. 13-16 The shoulder muscles of an Old World semibrachiator—*Colobus sp.*



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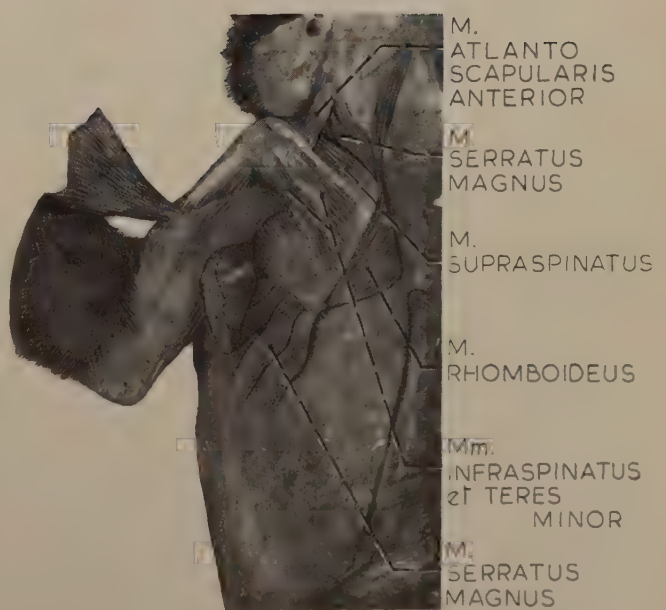


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5 CENTIMETRES



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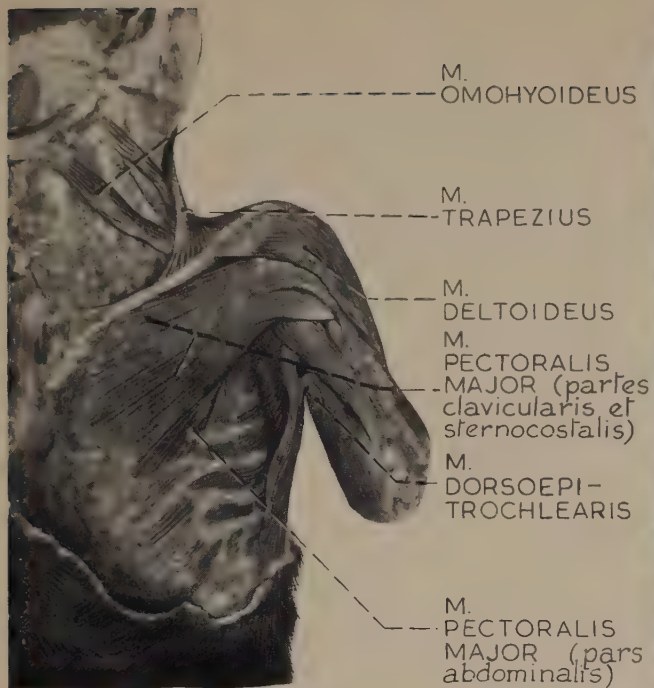
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Figs. 13-16. The shoulder muscles of an Old World semibrachiator—*Colobus* sp.

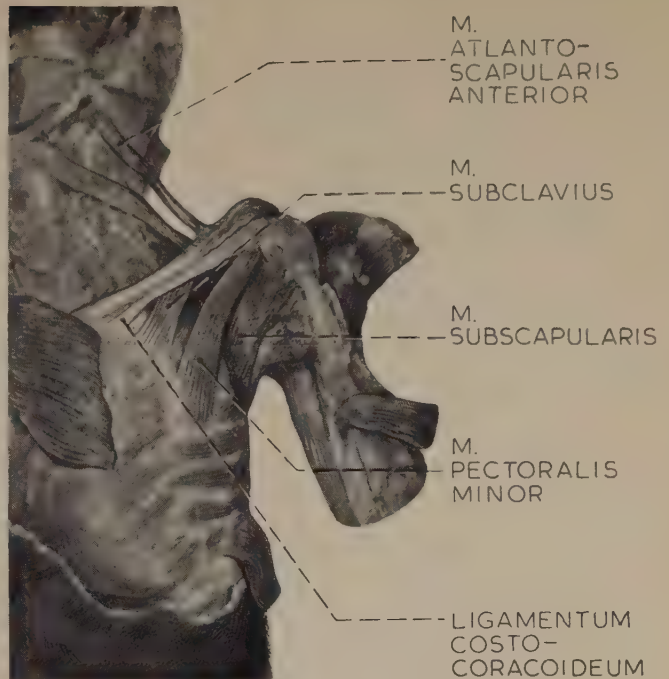
PLATE 5

PLATE 5

Figs. 17-20 The shoulder muscles of a brachiator (Hylobatinae)—*Hylobates* *sp.*

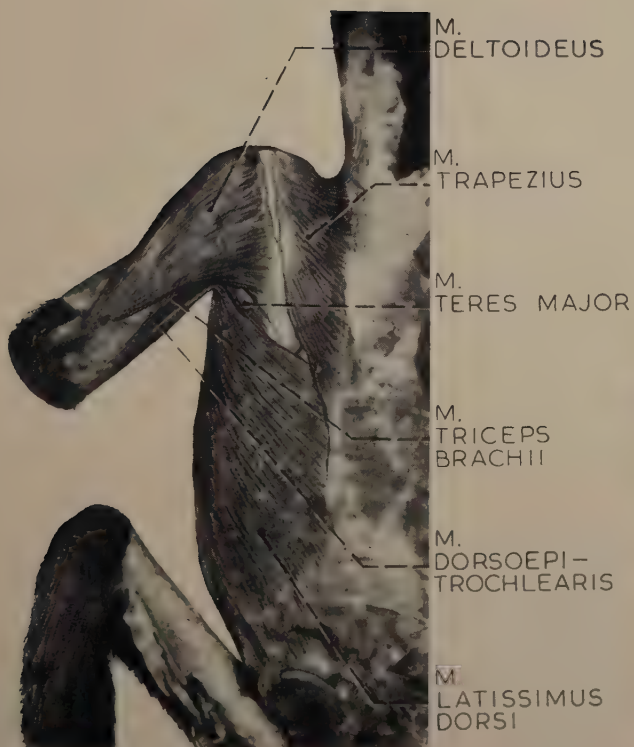


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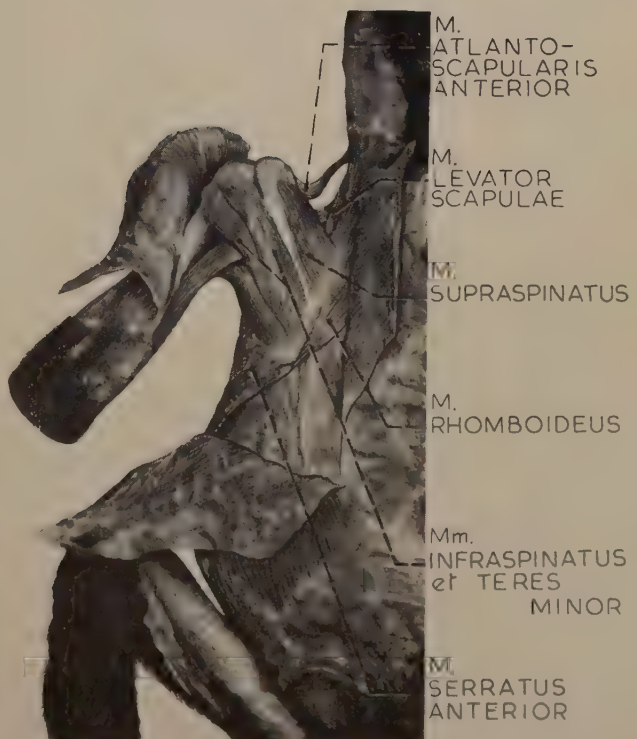


18

5 CENTIMETRES



19



20

Figs. 17-20. The shoulder muscles of a brachiator (Hylobatinae)—*Hylobates* sp.

PLATE 6

PLATE 6

Figs. 21-24 The shoulder muscles of a brachiator (Ponginae)—*Pongo pygmaeus*.



21



22

5 CENTIMETRES



23



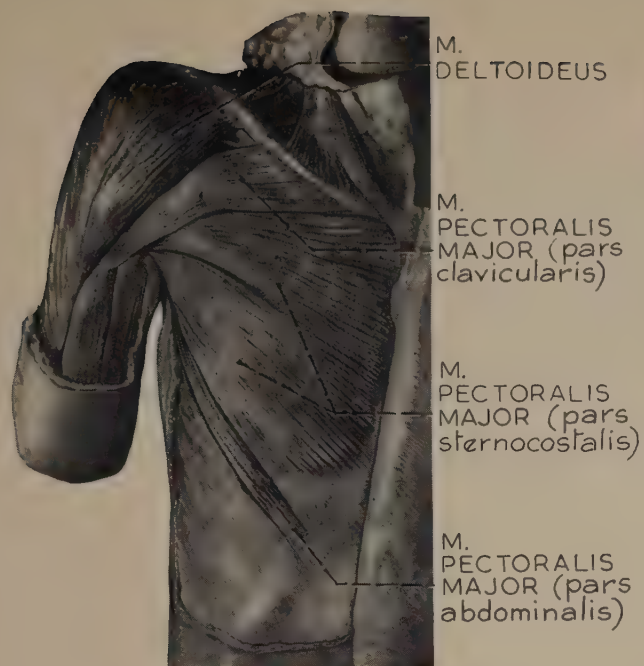
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Figs. 21-24. The shoulder muscles of a brachiator (Ponginae)—*Pongo pygmaeus*.

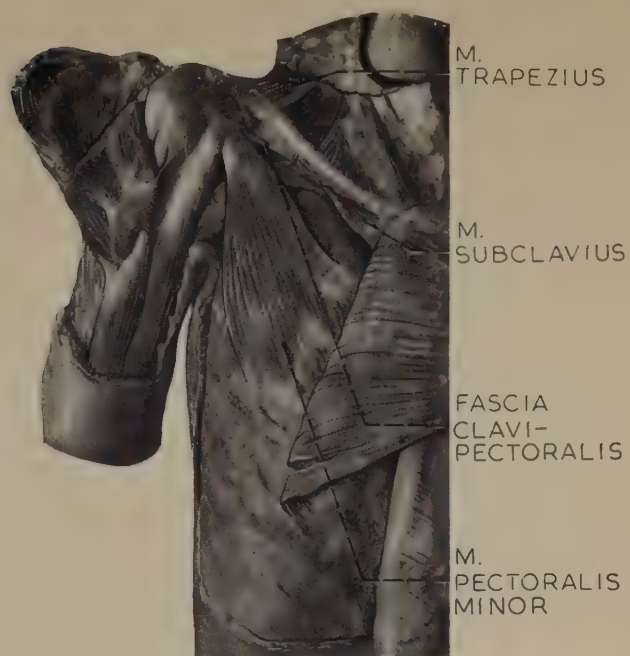
PLATE 7

PLATE 7

Figs. 25-28 The shoulder muscles of man (*Homo sapiens*).



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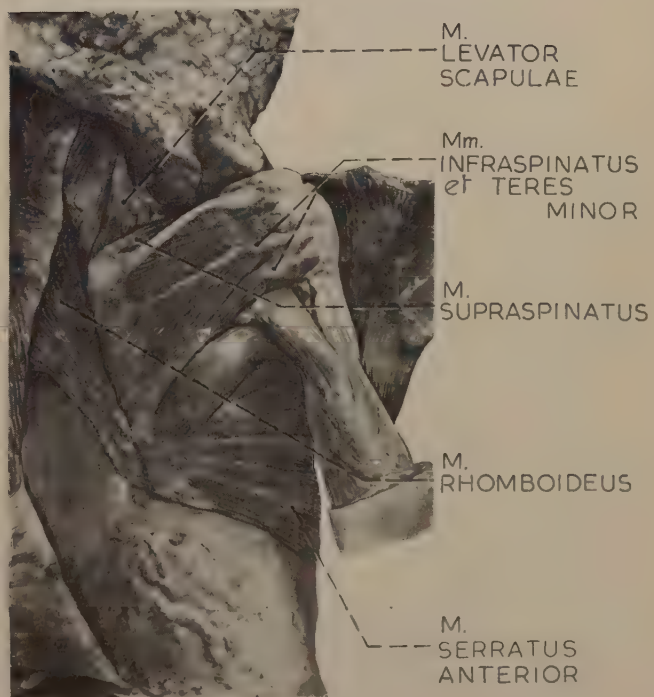


26

5 CENTIMETRES



27



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Figs. 25-28. The shoulder muscles of man (*Homo sapiens*).

Statistical Study
(ANTHROPOIDEA)

Tables and text figures

Basic statistical data relating to quadrupeds, semibrachiators, brachiators and man, are presented in Table 13. Text figures 29–32 summarize the results of comparisons between these four locomotor groups.

Ratios between, on the one hand, the various propulsive or arm-raising units, and on the other, the total weight of the stabilizers of the shoulder joint and scapula, are referred to as measuring the “relative size” of the units.

Muscles responsible for propulsion

The propulsive muscles are relatively bigger in brachiators and semibrachiators than in quadrupeds. But in man, they are no more developed than in quadrupeds (Fig. 29a).

The differences noted do not affect all units of the muscular group to an equal extent, because, in spite of the conspicuous morphological differences in the pectoral mass between locomotor groups, its relative size scarcely varies (Fig. 29b). But *m. latissimus dorsi* plus *m. teres major* is relatively bigger in semibrachiators and brachiators than in quadrupeds, while in man, it is smaller (Fig. 29c). The differences between the four locomotor groups in the development of, on the one hand, the pectoral mass and, on the other, *m. latissimus dorsi* plus *m. teres major* emerge clearly when the weights of these muscles are compared directly. In brachiators and semibrachiators, the weight of the pectoral mass relative to that of *m. latissimus dorsi* plus *m. teres major* is less than in quadrupeds, while in man it is significantly bigger (Fig. 29d).

Muscles responsible for raising the arm

The muscles responsible for raising the arm are relatively bigger in semibrachiators than in quadrupeds. They are bigger still in brachiators and in man which, in this respect, differ little from each other (Fig. 30a).

A corresponding pattern of difference between quadrupeds, semibrachiators and brachiators is seen when each of the main components of this muscle group [firstly abductors of the humerus—*m. deltoideus* (Fig. 30b) and secondly rotators of the scapula—*m. trapezius* together with *m. atlantoscapularis anterior* and *m. serratus magnus pars caudalis* (Fig. 30c)], are considered separately. But while, *m. deltoideus* is, so far as may be judged from the available data, of similar relative size in man and brachiators, *m. trapezius* plus *m. serratus magnus pars caudalis* is, in man, relatively smaller (Figs. 30b and c).

The ratio between the weight of the abductors of the humerus and the rotators of the scapula is similar in quadrupeds, semibrachiators and brachiators (Fig. 30d). This finding indicates that the extent of difference between these three locomotor groups is similar for each of these muscular components. The corresponding index

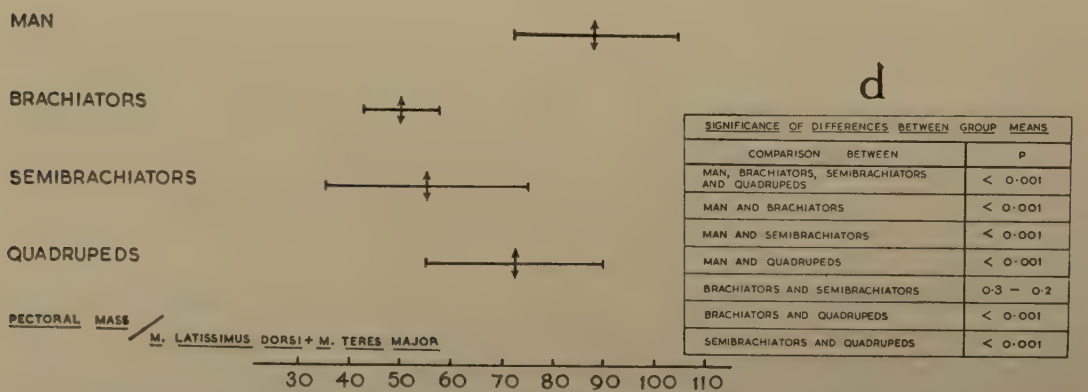
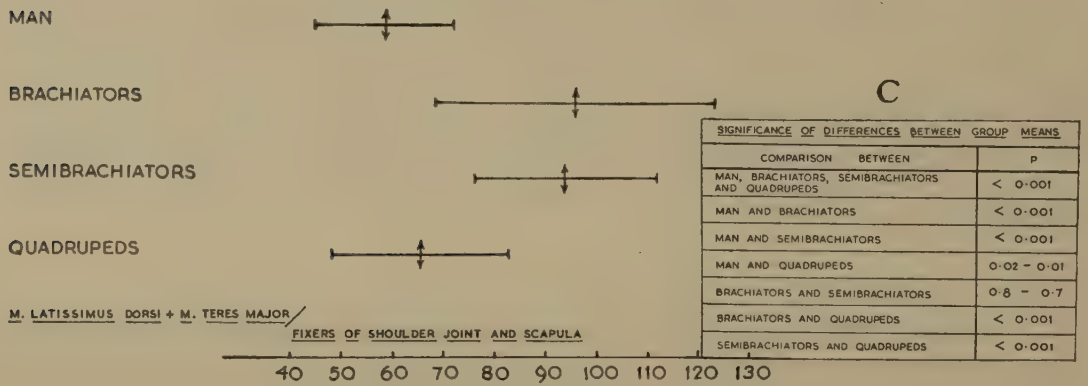
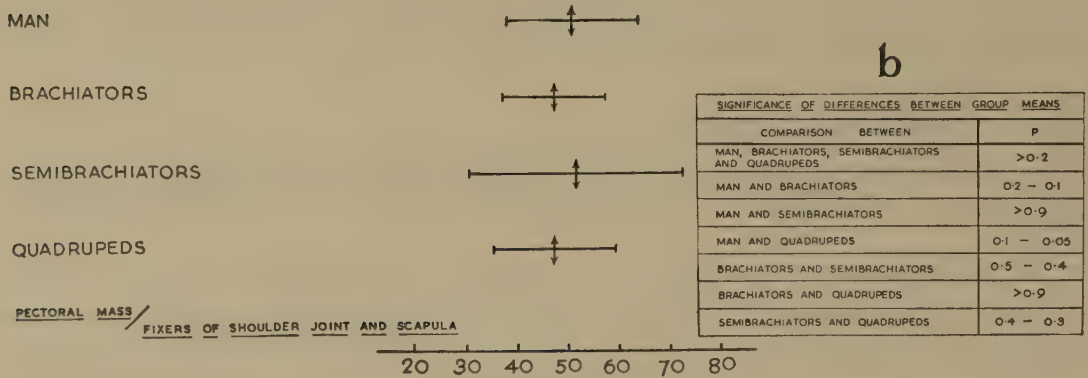
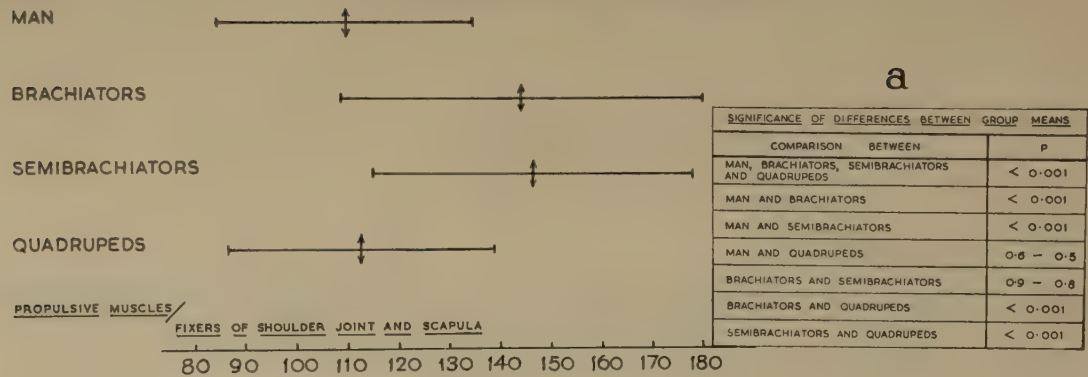


Fig. 29 The relative weights of the propulsive muscles in the Anthropeidea.

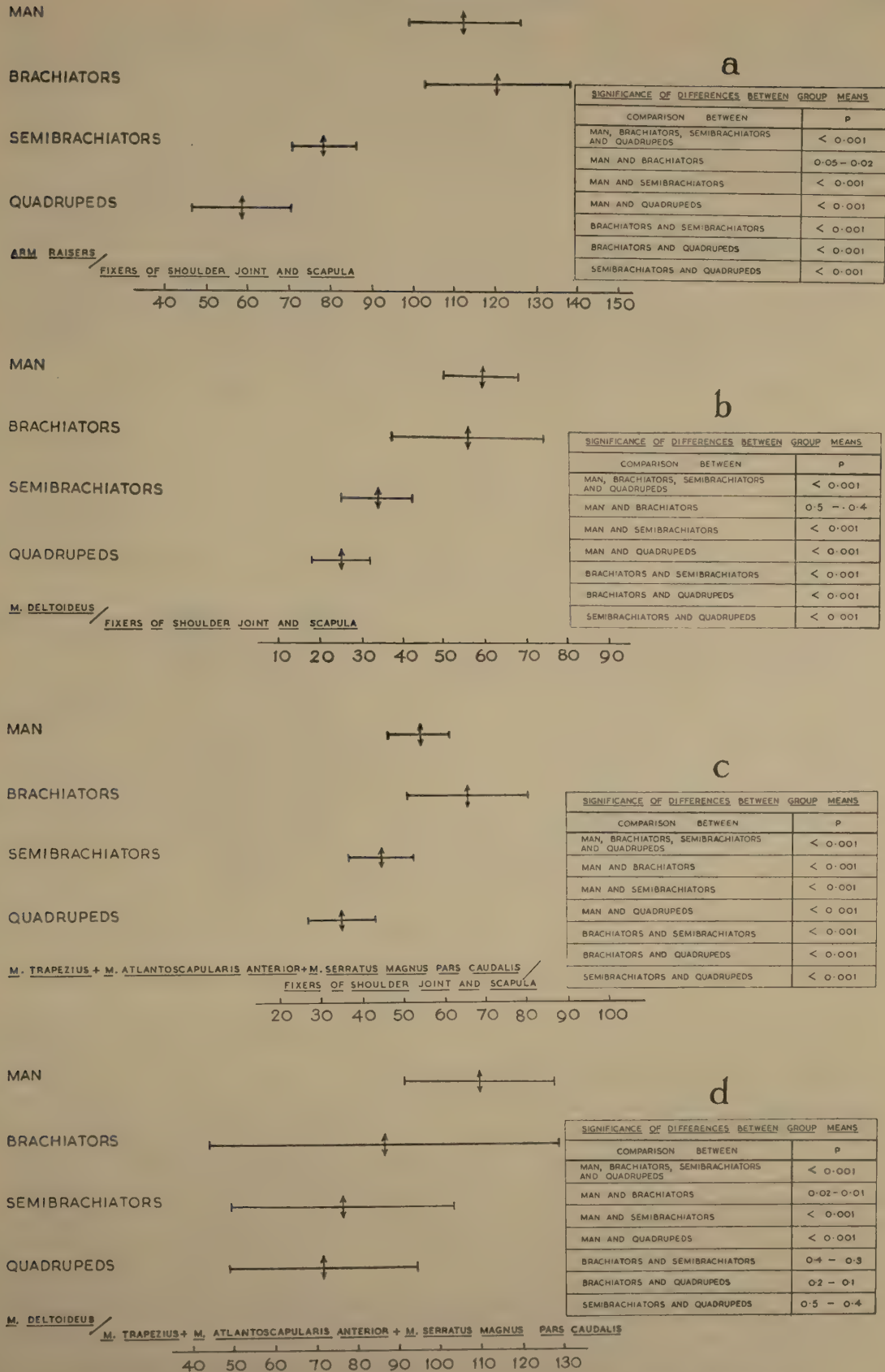


Fig. 30 The relative weights of the arm-raising muscles in the Anthropoidea.

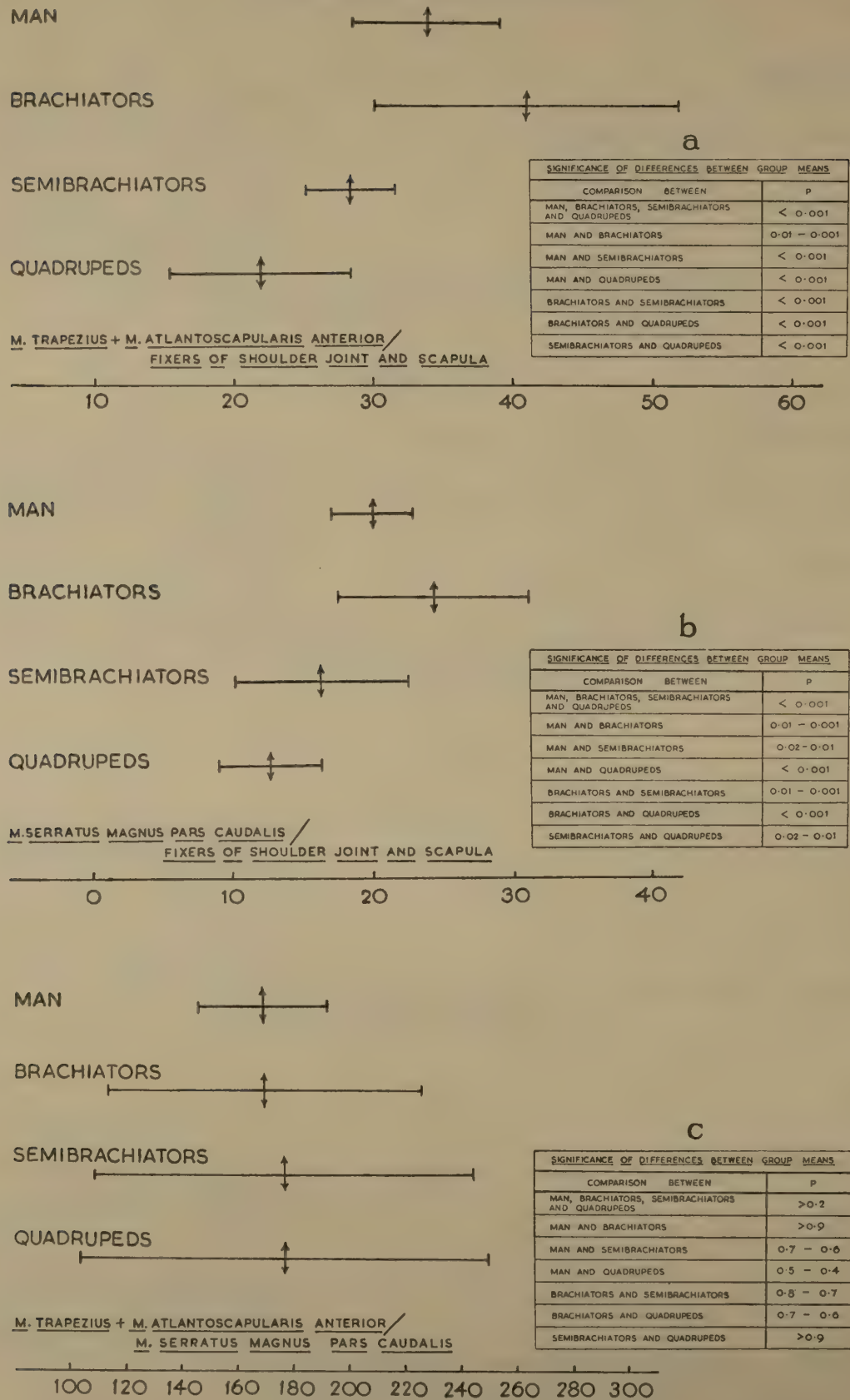


Fig. 31 The relative weights of the rotators of the scapula in the Anthropeidea.

is significantly bigger in man (Fig. 30b). This reflects the fact that the development of the abductors of the humerus is equivalent to that characteristic of brachiators, while the development of the rotators of the scapula is relatively weaker.

Within the subgroup comprising muscles responsible for rotating the scapula, the pattern of difference between quadrupeds, semibrachiators, brachiators and man seen in each of the main component units [firstly, m. trapezius together with m. atlantoscapularis anterior which form the upper arm of the force couple acting on the scapula (Fig. 31a), and secondly, m. serratus magnus pars caudalis which forms the corresponding lower arm (Fig. 31b)] is similar to that characteristic of the muscular subgroup as a whole. The ratio between the upper and lower arms of the force couple is similar in each of the four locomotor groups (Fig. 31c).

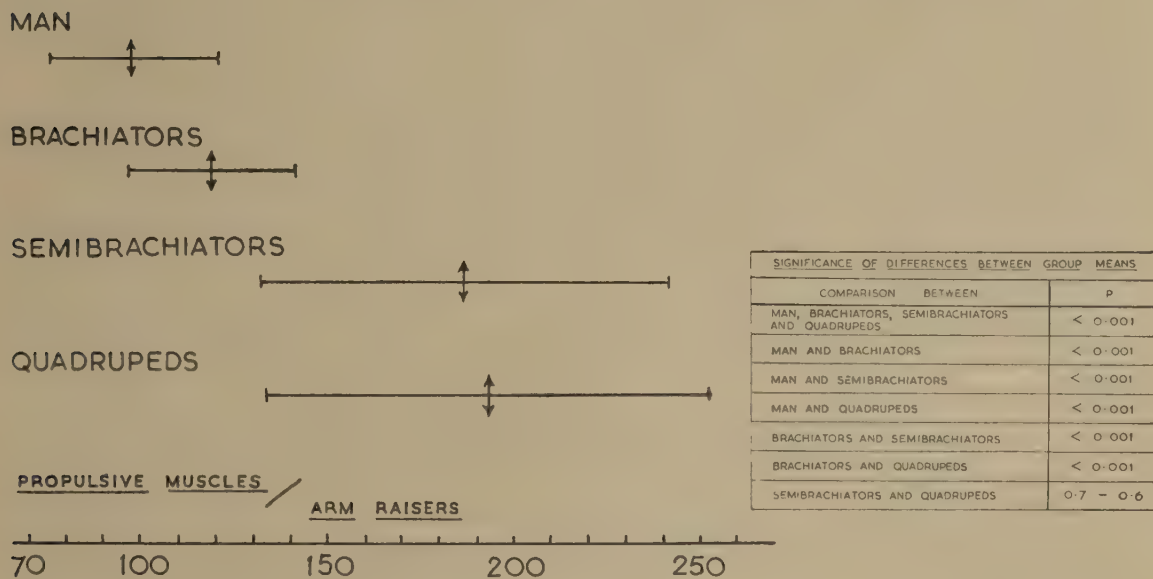


Fig. 32 The ratio of the weights of the propulsive and arm-raising muscles in the Anthropeidea.

Comparison between propulsive muscles and arm raisers (Fig. 32)

The mean value of the ratio between the weight of the propulsive muscles and that of the arm-raisers is similar in quadrupeds and semibrachiators. This finding indicates that the relative increase of the propulsive muscles in semibrachiators as compared with quadrupeds is similar to that of arm-raisers.

In brachiators, the ratio between the weights of the propulsive muscles and the arm-raisers is smaller than in semibrachiators or quadrupeds—a reflection of the relatively greater development, in brachiators, of the muscles responsible for raising the arm.

In man, this ratio is smaller than in any other locomotor group. This observation correlates with the findings that while the propulsive muscles are relatively as small as in quadrupeds, the arm-raisers are almost as big as in brachiators.

TABLE 13
Relative weights of shoulder muscles (Anthropoidea).

	QUADRUPEDS		SEMI-BRACHIATORS		BRACHIATORS		MAN	
	Mean	Number of specimens mean	Mean	Number of specimens mean	Mean	Number of specimens mean	Mean	Number of specimens mean
Propulsive muscles/fixers of shoulder joint and scapula	112.6	22	145.5	5	143.2	6	109.7	21
Pectoral mass/fixers of shoulder joint and scapula	47.1	22	51.6	5	47.4	6	51.2	21
M. latissimus dorsi + m. teres major/fixers of shoulder joint and scapula	65.5	22	93.9	5	95.8	6	58.5	21
Pectoral mass/m. latissimus dorsi + m. teres major	72.7	22	55.0	5	49.8	6	87.8	21
Arm raisers/fixers of shoulder joint and scapula	59.1	22	78.3	5	120.7	6	112.4	21
M. deltoideus/fixers of shoulder joint and scapula	24.5	22	33.7	5	55.4	6	58.6	21
M. trapezius + m. atlantoscaphularis anterior + m. serratus magnus pars caudalis/fixers of shoulder joint and scapula	34.6	22	44.6	5	65.3	6	53.8	21
M. deltoideus/m. trapezius + m. atlantoscaphularis anterior + m. serratus magnus pars caudalis	71.7	22	76.2	5	86.3	6	109.3	21
M. trapezius + m. atlantoscaphularis anterior/fixers of shoulder joint and scapula	21.9	22	28.2	5	40.9	6	33.8	21
M. serratus magnus pars caudalis/fixers of shoulder joint and scapula	12.7	22	16.4	5	24.4	6	20.0	21
M. trapezius + m. atlantoscaphularis anterior/m. serratus magnus pars caudalis	176.6	22	176.4	5	169.4	6	168.9	21
Propulsive muscles/arm raisers	193.1	22	186.5	5	118.5	6	97.8	21

Qualitative description of dissections
(PROSIMII)

Muscles responsible for propulsion

M. pectoralis major

General description: In the Prosimii, the principal features of *m. pectoralis major* are similar to those encountered in the Anthropoidea (p. 565) except that some superficial fibres blend with the ventral border of *m. deltoideus*.

Principal contrasts between locomotor groups (Pls. 8–10 and Table 14) : In quadrupeds, the origin of this triangular muscle is relatively long and the direction of the fibres, while to some extent lateral, is predominantly cranial.

In hangers, the origin is shorter and the direction of the fibres more lateral.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 33) : *M. pectoralis major* arose from the extreme medial end of the clavicle, the capsule of the sternoclavicular joint, all the sternebrae and the medial ends of the cartilages of certain of the false ribs. The caudal limit of origin usually varied between the seventh and ninth costal cartilages (Table 14). Huntington (1897) described a specimen of *Lemur* in which this limit was the eleventh costal cartilage, but in this case, there was no distinct *m. pectoralis abdominalis*. In our specimen of *Lemur*, in three specimens described by Huntington (1897) and Zuckercandl (1910) and in two of our four specimens of *Galago*, the muscle was divided by a fibrous raphe at the junction of the manubrium and the first sternebra. The muscle was undivided in the remaining specimens of *Galago*, in the specimen of *Tupaia*, and in six specimens of *Tupaia* and *Ptilocercus* described by Le Gros Clark (1924, 1926).

The muscle was of approximately uniform thickness throughout. Its cranial fibres passed mainly laterally, but the remainder passed cranially and to some extent laterally. The insertion did not vary.

(b) *hangers:* (Pl. 9, fig. 37 and Pl. 10, fig. 41) : The origin of *m. pectoralis major* was restricted to the extreme medial end of the clavicle, the capsule of the sternoclavicular joint and the first six sternebrae (Table 14). In a specimen of *Nycticebus* described by Tschachmachtschjan (1911) there was no distinct *m. pectoralis abdominalis* and the caudal limit of origin of *m. pectoralis major* lay at the level of the eighth sternocostal joint.

No variations were observed in either the direction of *m. pectoralis major* or in its insertion.

In one of our two specimens of *Nycticebus* and in that of *Perodicticus*, the muscle was divided by a fibrous raphe level with the caudal edge of the manubrium. In the specimen of *Propithecus*, a similar fibrous raphe was level with the joint between the second and third sternebrae. In the second specimen of *Nycticebus*, *m. pectoralis major* was undivided.

M. pectoralis major was uniformly thick in *Nycticebus* and *Perodicticus*, but in *Propithecus*, its cranial part was the thicker.

TABLE 14
Variation in the origin of *m. pectoralis major* (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs				
	Present study	Literature*	5	6	7	8	9
Quadrupeds ..	6	22	—	7.1	7.1	78.6	7.1
Hangers ..	4	9	—	100.0	—	—	—

Significance of difference in mean caudal limit of origin of *m. pectoralis major* : Quadrupeds and Hangers : $P < 0.001$.

* Clark 1926 ; Huntington 1897, 1903 ; Miller 1943 ; Mivart & Murie 1865 ; Murie & Mivart 1872 ; Tschachmachtschjan 1911 ; Woollard 1925 ; Zuckercandl 1910.

M. pectoralis minor

General description: The general configuration of *m. pectoralis minor* (p. 568) is similar in both the Prosimii and the Anthropoidea.

Principal contrasts between locomotor groups: (Pls. 8–10 and Table 15) : In the specimens studied, there appeared to be no correlation between muscular variation and locomotor groupings.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 34) : *M. pectoralis minor* took origin, on average, from the second to sixth costal cartilages and from the adjoining sternebrae (Table 15).

M. pectoralis minor was usually distinct from *m. pectoralis major*. But Murie and Mivart (1872) have reported that in *Lemur*, the caudal borders of the two muscles may be conjoined close to their origin, and that in *Galago*, the two muscles may be completely fused along their line of origin. Le Gros Clark (1926) found a similar extensive fusion in four specimens of *Ptilocercus*.

The fibres passed cranio-laterally to be inserted into the capsule of the shoulder joint. Lander (1918) described single specimens of *Tupaia* and *Daubentonia* in which *m. pectoralis minor* inserted into the coracoid process.

(b) *hangers:* (Pl. 9, fig. 38 and Pl. 10, fig. 42) : *M. pectoralis minor* displayed the same origin as in quadrupeds (Table 15).

In *Perodicticus* and *Propithecus*, the caudal border of the muscle was fused near its origin with *m. pectoralis major*.

The direction and insertion of *m. pectoralis minor* were similar to those characteristic of quadrupeds. Murie and Mivart (1872) reported insertions of *m. pectoralis minor* typically confined to the lesser tuberosity in *Loris* and *Nycticebus* and to the greater tuberosity in *Perodicticus*. Barnard (1875) reported in *Loris* and *Perodicticus*, insertions restricted to the lesser tuberosity.

TABLE 15
Variation in the origin of m. pectoralis minor (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from ribs			
	Present study	Literature*	1	2	3	4
Quadrupeds ..	6	22	—	75.0	7.1	17.9
Hangers ..	4	9	—	92.3	7.7	—

Significance of difference in mean cranial limit of m. pectoralis minor : Quadrupeds and Hangers : $P=0.05-0.02$.

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs			
	Present study	Literature*	5	6	7	8
Quadrupeds ..	6	22	—	60.7	35.7	3.6
Hangers ..	4	6	10.0	50.0	20.0	20.0

Significance of difference in mean caudal limit of origin of m. pectoralis minor : Quadrupeds and Hangers : $P=0.9-0.8$.

Locomotor group	Number of specimens		Percentage of cases in which ribs were spanned			
	Present study	Literature*	4	5	6	7
Quadrupeds ..	6	22	17.9	67.9	10.7	3.5
Hangers ..	4	6	10.0	50.0	30.0	10.0

Significance of difference in mean numbers of ribs spanned by m. pectoralis minor : Quadrupeds and Hangers : $P=0.2-0.1$.

* Clark 1924, 1926 ; Huntington 1897, 1903 ; Miller 1943 ; Murie & Mivart 1872 ; Tschachmachtschjan 1911 ; Zuckercandl 1910.

M. pectoralis abdominalis

General description: The general description of m. pectoralis abdominalis given for the Anthropoidea (p. 570) applies also to the Prosimii.

Principal contrasts between locomotor groups: (Pls. 8-10 and Table 16) : In quadrupeds, m. pectoralis abdominalis is thicker and has a more extensive origin than in hangers.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 34) : M. pectoralis abdominalis arose from three costal cartilages caudal to m. pectoralis major (Table 16), adjacent fibres of the two muscles fusing close to their origins. In one of our four specimens of

Galago, m. pectoralis abdominalis and m. pectoralis minor were fused along the entire length of their adjacent borders, and m. pectoralis major was discrete.

M. pectoralis abdominalis was almost as thick as m. pectoralis major and passed cranially to be inserted into the capsule of the shoulder joint.

In one specimen of *Lemur* described by Huntington (1897) and in one of *Galago* described by Tschachmachtschjan (1911), m. pectoralis abdominalis was not present as a separate muscle.

TABLE 16
Variation in the origin of m. pectoralis abdominalis (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from ribs			
	Present study	Literature*	5	6	7	8
Quadrupeds ..	6	15	9.5	—	—	90.5
Hangers ..	4	8	—	—	100.0	—

Significance of difference in mean cranial limit of origin of m. pectoralis abdominalis : Quadrupeds and Hangers : $P=0.01-0.001$.

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs				
	Present study	Literature*	7	8	9	10	11
Quadrupeds ..	6	15	—	—	9.5	76.2	14.3
Hangers ..	4	4	12.5	50.0	37.5	—	—

Significance of difference in mean caudal limit of origin of m. pectoralis abdominalis : Quadrupeds and Hangers : $P<0.001$.

Locomotor group	Number of specimens		Percentage of cases in which ribs were spanned				
	Present study	Literature*	1	2	3	4	5
Quadrupeds ..	6	15	—	—	76.2	14.3	9.5
Hangers ..	4	4	12.5	50.0	37.5	—	—

Significance of difference in mean numbers of ribs spanned by m. pectoralis abdominalis : Quadrupeds and Hangers : $P<0.001$.

* Clark 1926 ; Huntington 1903 ; Miller 1943 ; Murie & Mivart 1872 ; Tschachmachtschjan 1911 ; Woollard 1925.

(b) *hangers*: (Pl. 9, fig. 38 and Pl. 10, fig. 42) : In our specimens of *Nycticebus* and *Perodicticus*, m. pectoralis abdominalis took origin from two costal cartilages caudal to m. pectoralis major (Table 16). In the specimen of *Propithecus*, the muscle

arose from a single cartilage only, there being a gap of one cartilage between its origin and that of *m. pectoralis major*.

In *Nycticebus* and *Perodicticus*, *m. pectoralis abdominalis* was thinner than *m. pectoralis major*—a contrast even more marked in *Propithecus*.

In *Nycticebus* and *Perodicticus*, the fibres were directed laterally, but in *Propithecus*, their direction was, as in quadrupeds, more cranial.

No variations were found in the pattern of insertion.

In one specimen of *Nycticebus* described by Tschachmachtschjan (1911), *m. pectoralis abdominalis* was absent.

The pectoral mass (Table 17)

In quadrupeds, the origin of the triangular mass comprising *m. pectoralis major*, *m. pectoralis minor* and *m. pectoralis abdominalis* is long and of uniform thickness. It extends caudally to the tenth or eleventh costal cartilage. In hangers, its origin is shorter, its caudal part is thinner and usually extends to the eighth costal cartilage only.

TABLE 17
Variation in the caudal limit of the pectoral mass (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs				
	Present study	Literature*	7	8	9	10	11
Quadrupeds ..	6	16	—	—	9.1	72.7	18.2
Hangers ..	4	5	11.1	55.6	33.3	—	—

Significance of difference in mean caudal limit of origin of the pectoral mass : Quadrupeds and Hangers : $P < 0.001$.

* Clark 1926 ; Huntington 1897, 1903 ; Miller 1943 ; Murie & Mivart 1872 ; Tschachmachtschjan 1911 ; Woollard 1925.

M. latissimus dorsi

General description: The general features of *m. latissimus dorsi* (p. 574) do not differ between the Prosimii and the Anthropoidea.

Principal contrasts between locomotor groups: (Pls. 8–10 and Table 18) : In quadrupeds, *m. latissimus dorsi* is thin and its origin is restricted to the mid-line of the dorsum of the trunk. Its fibres pass cranio-ventrally.

In hangers, the muscle is thick, especially in its caudal part, and its origin extends on to the lateral aspect of the trunk. The caudal fibres are directed more cranially and less ventrally than in quadrupeds.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 35) : The cranial limit of origin of *m. latissimus dorsi* varied between the fifth and seventh thoracic spines (Table 18). The caudal fibres arose from the fascia thoracolumbalis, through which they were attached to the vertebral spines, extending caudally to the mid-lumbar region.

In *Tarsius*, a few caudal fibres may take origin from the most posterior part of the iliac crest (Hill 1955). In the two specimens of *Ptilocercus* described by Le Gros Clark (1926), small muscular slips arose from the lower three ribs to fuse with the deep surface of the muscle. Hill (1953) records similar slips from the lower four ribs in *Daubentonia*.

In all cases, *m. latissimus dorsi* was thin, and its insertion followed the pattern characteristic of the Primates as a whole.

In one of our four specimens of *Galago*, in our single specimen of *Tupaia* and in two further specimens described by Le Gros Clark (1924), fleshy fibres, detached from the muscle near the base of the tendon of insertion, blended with those of *m. teres major*.

The features of *m. latissimus dorsi* recorded by Dzwonkowski (1937) in ten specimens of *Lemur* agree with those described in the present study as typical of quadrupedal prosimians.

TABLE 18
Variation in the origin of *m. latissimus dorsi* (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from the spine of			
	Present study	Literature*	T.5	T.6	T.7	T.8
Quadrupeds ..	6	18	37.5	37.5	25.0	—
Hangers ..	4	5	—	—	77.8	22.2

Significance of difference in mean cranial limit of origin of *m. latissimus dorsi* : Quadrupeds and Hangers : $P < 0.001$.

Locomotor group	Number of specimens		Percentage of cases in which slips came from				
	Present study	Literature*	0	1	2	3	4
Quadrupeds ..	6	18	83.3	—	—	16.7	—
Hangers ..	4	8	41.7	—	25.0	25.0	8.3

Significance of difference in mean numbers of slips taking origin from the ribs : Quadrupeds and Hangers : $P = 0.05-0.02$.

* Clark 1924, 1926 ; Miller 1943 ; Murie & Mivart 1872 ; Schuck 1912 ; Woollard 1925.

(b) *hangers*: (Pl. 9, fig. 39 and Pl. 10, fig. 43) : The cranial limit of origin was usually the seventh thoracic spine (Table 18). The more caudal parts of the muscle gained attachment through the fascia thoracolumbalis both to the lumbar vertebrae and sacrum and to the whole of the short iliac crest. Additional fibres arose as bundles from the lower ribs (Table 18), forming the ventral edge of the muscle and extending to the mid-axillary line.

As the most ventral fibres of *m. latissimus dorsi* were attached to the lateral aspect of the trunk, they were always directed more cranially than in quadrupeds.

In our specimens, and especially in *Propithecus*, *m. latissimus dorsi* was thicker than in quadrupeds. The insertion displayed no noteworthy variations from the typical primate pattern.

M. dorsoepitrochlearis

General description: In the Prosimii, the principal features of *m. dorsoepitrochlearis* are similar to those characteristic of the Anthropoidea (p. 577).

Principal contrasts between locomotor groups: (Pls. 8–10): In quadrupeds, *m. dorsoepitrochlearis* inserts distal to the elbow joint; in hangers, the insertion is normally proximal.

Variation: (a) *quadrupeds:* (Pl. 8, figs. 33 and 35): In our specimen of *Lemur* and in three of the four specimens of *Galago*, *m. dorsoepitrochlearis* took origin as in the other Primates. In the remaining specimen of *Galago*, in *Tupaia* and in a specimen of *Ptilocercus* described by Le Gros Clark (1926), where an interchange of fibres occurred between *m. latissimus dorsi* and *m. teres major*, *m. dorsoepitrochlearis* received contributions from each. In a specimen of *Tupaia* described by Le Gros Clark (1924), where similar interconnections between *m. latissimus dorsi* and *m. teres major* were found, *m. dorsoepitrochlearis* comprised two separate bellies, one from each muscle.

M. dorsoepitrochlearis passed down the dorso-medial aspect of the arm to be attached to the olecranon and medial epicondyle. A strong aponeurotic sheet passed between these two points and gained insertion into the fascia on the extensor aspect of the forearm.

In the specimens of *Lemur*, *Galago*, *Daubentonia* and *Tarsius* described by Breinl (1958) and in the account of *Tarsius* given by Hill (1955), *m. dorsoepitrochlearis* was described as inserting into the tip of the olecranon along with *m. triceps brachii*. An insertion into the olecranon and posterior border of the ulna may occur in *Lemur* (Hill 1953).

(b) *hangers:* (Pl. 9, fig. 37 and Pl. 10, figs. 41 and 43): In the available specimens, no variations were recorded either in the origin or direction of *m. dorsoepitrochlearis*. In *Nycticebus*, the fibres inserted into the fascia covering the intermediate third of *m. triceps brachii*, and in *Perodicticus* and *Propithecus*, into the medial epicondyle. In the specimen of *Nycticebus*, dissected by Schuck (1913), the insertion was into the medial border of the olecranon. Edwards and Grandidier (1875) recorded for *Propithecus* the additional insertion of some few aponeurotic fibres into the fascia of the forearm.

M. teres major

General description: The general configuration of *m. teres major* (p. 578) is similar in both the Prosimii and the Anthropoidea.

Principal contrasts between locomotor groups: (Pls. 8–10) : In quadrupeds, m. teres major is relatively bigger than in hangers.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 36) : M. teres major took origin from an appreciable area near the inferior angle of the scapula and from most of the lateral border. There were no variations in the direction of its fibres.

The only variation in insertion occurred in certain specimens of *Tupaia* and *Galago* where, as already noted (p. 622), this muscle received a slip from m. latissimus dorsi.

(b) *hangers:* (Pl. 9, fig. 37 and Pl. 10, fig. 43) : M. teres major arose from a small area around the inferior angle of the scapula and from a short adjoining part of the lateral border. In general characters and mode of insertion, the muscle was constant.

Muscles responsible for raising the arm

M. deltoideus

General description: In the Prosimii, the principal features of m. deltoideus are similar to those in the Anthropeidea (p. 579), except that the ventral border is fused with the superficial part of m. pectoralis major.

Principal contrasts between locomotor groups: (Pls. 8–10) : In quadrupeds, m. deltoideus is small. Its three heads are discrete and are inserted into the proximal third of the humerus.

In hangers, the muscle is bigger, the separation between the heads is less marked and the insertion reaches approximately half-way down the humerus.

Variation: (a) *quadrupeds:* (Pl. 8, figs. 33 and 35) : The pars clavicularis arose from the lateral quarter of the clavicle ; the pars acromialis was attached to the acromion and the overlying fascial sheet, while the pars spinalis took origin from the lateral half of the scapular spine. The three heads were separated by triangular spaces containing loose areolar tissue.

In six specimens of *Tupaia* and *Ptilocercus* (Le Gros Clark 1924, 1926) and in two specimens of *Tarsius* (Woollard 1925), m. deltoideus comprised pars clavicularis and pars acromialis only, the origin of the latter extending on to the lateral part of the spine of the scapula.

The mode of insertion of m. deltoideus did not differ from that characteristic of other Prosimii.

(b) *hangers:* (Pl. 9, figs. 37 and 39 and Pl. 10, figs. 41 and 43) : In *Nycticebus* and *Propithecus* the pars clavicularis took origin from the lateral two-thirds of the clavicle. In *Perodicticus*, some of its superficial fibres took origin from a fibrous raphe lying between m. trapezius and the pars clavicularis of m. deltoideus as these joined on the ventral aspect of the clavicle.

The pars acromialis showed no noteworthy variations, but the pars spinalis arose, not only from the lateral two-thirds of the scapular spine, but also from the fascia covering m. infrapinatus.

The three heads of *m. deltoideus* were joined by fibrous raphes and inserted into a deltoid tuberosity approximately half-way along the humerus.

M. trapezius

General description: The general description of *m. trapezius* given for the Anthro-poidea (p. 581) applies to the Prosimii.

Principal contrasts between locomotor groups: (Pls. 8–10 and Table 19) : In quadrupeds, the cranial part of *m. trapezius* is no thicker than the caudal region ; the fibres pass in a predominantly caudal direction to insert into the acromion and into the scapular spine which lies at right angles to the vertebral column.

In hangers, the cranial part of *m. trapezius* is considerably thicker than the caudal part ; it passes more laterally than in quadrupeds and inserts into the lateral part of the clavicle, the acromion and the lateral half of the obliquely-placed scapular spine.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 35) : The cranial part of *m. trapezius* took origin from a short part of the nuchal crest close to the mid-line, the external occipital protuberance and the ligamentum nuchae. In the two specimens of *Tarsius* described by Woollard (1925), the cranial limit of origin was the middle of the ligamentum nuchae.

The caudal limit of origin lay most frequently at the level of the ninth thoracic vertebra (Table 19).

The cranial part of the muscle was uniformly thin and its fibres passed caudally to meet the spine of the scapula at approximately right angles. They were inserted into its entire length and, except in the specimen of *Tupaia*, into the acromion.

In all genera except *Tupaia*, the intermediate part of *m. trapezius* was aponeurotic and passed almost horizontally to be inserted near the medial end of the spine of the scapula. In *Tupaia*, however, the distal parts of the intermediate fibres were fleshy and the aponeurotic area of origin therefore triangular.

The fibres of the caudal part of the muscle were as thick as in the cranial region ; they were fleshy throughout and passed cranially to be inserted into and around a well-marked tubercle close to the medial end of the scapular spine.

(b) *hangers:* (Pl. 9, fig. 39 and Pl. 10, fig. 43) : The cranial part of *m. trapezius* was fused with the most dorsal fibres of *m. sternocleidomastoideus* close to their origin. In *Perodicticus*, the region of fusion lay on the superior nuchal line, in *Nycticebus*, on the external occipital protuberance, and in two specimens of *Perodicticus* described by Miller (1943) on the ligamentum nuchae level with the second cervical spine. In *Propithecus*, the cranial limit of origin of *m. trapezius* was level with the spine of the axis, but its fibres were independent of *m. sternocleidomastoideus*.

In *Nycticebus* and *Perodicticus*, there was a triangular aponeurosis in the upper thoracic region but in *Propithecus*, the whole muscle was fleshy.

The caudal part of the muscle took origin from the lower thoracic spines, variations in the caudal limit of origin being summarized in Table 19.

In all cases, and especially in *Perodicticus*, the cranial part of *m. trapezius* was

much the thickest. These fibres passed laterally to be inserted into the lateral half of the scapular spine, the acromion and the lateral third of the clavicle. In *Perodicticus*, the insertion extended over the lateral two-thirds of the clavicle, some fibres blending with those of m. deltoideus (p. 624). In all cases, and especially in *Perodicticus*, the clavicular part of the muscle was even more strongly developed than the rest of its cranial region.

In *Nycticebus* and *Perodicticus*, the intermediate part of m. trapezius comprised aponeurotic fibres interspersed with a few muscular elements. For seven specimens of *Perodicticus*, *Loris* and *Nycticebus*, Miller (1943) described this region as completely aponeurotic; in our specimen of *Propithecus*, it was thin but entirely fleshy. In all cases, the intermediate part of m. trapezius inserted into the intermediate third of the spine of the scapula.

The fleshy caudal component of m. trapezius was uniformly thin, with fibres passing cranially to a short aponeurosis inserted into a pronounced tubercle at the junction of the intermediate and medial thirds of the scapular spine.

TABLE 19
Variation in the origin of m. trapezius (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from the spine of			
	Present study	Literature*	T.9	T.10	T.11	T.12
Quadrupeds ..	6	22	42.9	42.9	10.7	3.5
Hangers ..	4	8	16.7	50.0	25.0	8.3

Significance of difference in mean caudal limit of origin of m. trapezius : Quadrupeds and Hangers : $P=0.2-0.1$.

* Clark 1924, 1926; Dzwonkowski 1935; Miller 1943; Murie & Mivart 1872; Schuck 1913; Woollard 1925.

M. atlantoscapularis anterior

General description: The general features of m. atlantoscapularis anterior (p. 584) do not differ between the Prosimii and Anthropoidea.

Principal contrasts between locomotor groups: (Pls. 8-10) : In quadrupeds, m. atlantoscapularis anterior passes caudally and inserts into the acromion or metacromion. In hangers (when the muscle is present), it passes mainly laterally and inserts into the clavicle.

Variation: (a) *quadrupeds:* (Pl. 8, figs. 33 and 35) : The origin of m. atlantoscapularis anterior did not deviate from the pattern characteristic of other Prosimii. Its general direction was predominantly caudal and it lay superficial to m. trapezius.

M. atlantoscapularis anterior usually inserted into the metacromion. But in our specimen of *Tupaia*, in two specimens described by Le Gros Clark (1924), and in the two specimens of *Tarsius* described by Woollard (1925), the insertion was

into the acromion. No acromial insertion occurred in four specimens of *Ptilocercus* described by Le Gros Clark (1926).

(b) *hangers*: (Pl. 9, figs. 37 and 39) : In *Nycticebus*, m. atlantoscaphularis anterior took origin from the lateral mass of the atlas. It passed laterally and superficially to be inserted into the lateral part of the clavicle. In the specimens of *Loris* described by Miller (1943), the muscle inserted into the capsule of the acromio-clavicular joint.

In our specimens of *Propithecus* and *Perodicticus* and in *Perodicticus* as described by Murie and Mivart (1872), m. atlantoscaphularis anterior was absent.

TABLE 20
Variation in the origin of m. serratus magnus pars caudalis (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the cranial limit of origin was from ribs			
	Present study	Literature*	3	4	5	6
Quadrupeds ..	6	4	—	80.0	—	20.0
Hangers ..	4	8	25.0	50.0	25.0	—

Significance of difference in mean cranial limit of origin of m. serratus magnus pars caudalis : Quadrupeds and Hangers : $P=0.3-0.2$.

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from ribs						
	Present study	Literature*	7	8	9	10	11	12	13
Quadrupeds ..	6	18	4.2	70.8	16.7	8.3	—	—	—
Hangers ..	4	8	—	—	—	33.3	25.0	25.0	16.7

Significance of difference in mean caudal limit of origin of m. serratus magnus pars caudalis : Quadrupeds and Hangers : $P<0.001$.

Locomotor group	Number of specimens		Percentage of cases in which ribs were spanned				
	Present study	Literature*	5	6	7	8	9
Quadrupeds ..	6	4	90.0	10.0	—	—	—
Hangers ..	4	8	—	—	8.3	58.3	33.3

Significance of difference in mean numbers of ribs spanned by m. serratus magnus pars caudalis : Quadrupeds and Hangers : $P<0.001$.

* Clark 1924, 1926 ; Huntington 1897 ; Miller 1943 ; Murie & Mivart 1872 ; Schuck 1913 ; Woollard 1925.

M. serratus magnus pars caudalis

General description: In the Prosimii, the principal features of *m. serratus magnus pars caudalis* are similar to those of the Anthropeidea (p. 586).

Principal contrasts between locomotor groups: (Pls. 8–10 and Table 20) : In quadrupeds, *m. serratus magnus pars caudalis* comprises an average of five muscular slips, whose length and thickness do not differ markedly from the fasciculi comprising the *pars cranialis*.

In hangers, there are usually eight digitations, each longer and thicker than in the *pars cranialis*.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 36) : *M. serratus magnus pars caudalis* arose from the fourth to eighth ribs inclusive (Table 20) and was approximately as thick as the *pars cranialis*.

(b) *hangers:* (Pl. 9, fig. 40 and Pl. 10, fig. 44) : In *Nycticebus* and *Perodicticus*, *m. serratus magnus pars caudalis* comprised nine fasciculi, but in *Propithecus*, seven. Variations in the level of origin are summarized in Table 20. The fasciculi in the *pars caudalis* were always longer and thicker than in the *pars cranialis*.

*Muscles responsible for stabilizing the shoulder joint**M. supraspinatus*

General description: The general configuration of *m. supraspinatus* (p. 588) is similar in both the Prosimii and Anthropeidea.

Principal contrasts between locomotor groups: (Pls. 8–10) : In quadrupeds, *m. supraspinatus* although thicker, appears narrower than in hangers.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 36) : In *Galago*, *m. supraspinatus* was even narrower than in *Lemur* and *Tupaia*.

(b) *hangers:* (Pl. 9, fig. 40 and Pl. 10, fig. 44) : No noteworthy variations were observed.

Mm. infraspinatus et teres minor

General description: The general description of *mm. infraspinatus et teres minor* given for the Anthropeidea (p. 588) applies also to the Prosimii.

Principal contrasts between locomotor groups: (Pls. 8–10) : In quadrupeds, *mm. infraspinatus et teres minor* appear narrower and thicker than in hangers.

Variation: (Pl. 8, fig. 36 ; Pl. 9, fig. 40 and Pl. 10, fig. 44) : No noteworthy variations were found in any of the specimens of either quadrupeds or hangers, and none appear to have been reported in the literature.

M. subscapularis

General description: The general features of *m. subscapularis* (p. 589) do not differ between the Prosimii and the Anthropeidea.

Principal contrasts between locomotor groups: (Pl. 9) : No apparent contrasts exist between the four locomotor groups in any of the characters of this muscle.

Variation: (Pl. 9, fig. 38) : The features of m. subscapularis appeared constant in all specimens of both quadrupeds and hangers.

Muscles responsible for stabilizing the shoulder girdle

M. rhomboideus

General description: In the Prosimii, the principal features of m. rhomboideus are similar to those characteristic of the Anthropoidea (p. 589).

Principal contrasts between locomotor groups: (Pls. 8–10 and Table 21): M. rhomboideus is similar in quadrupeds and hangers.

Variation: (a) *quadrupeds:* (Pl. 8, fig. 36) : Except in *Tupaia*, the cranial part of m. rhomboideus arose from the medial third of the superior nuchal line and the external occipital protuberance. It was separated from the remainder of the muscle by a triangular gap filled with loose areolar tissue.

In both specimens of *Tarsius* described by Woollard (1925), the gap between the cranial and caudal parts was reduced to a narrow band of loose areolar tissue at the level of the second cervical spine. In these cases, the origin of the cranial part of this muscle extended caudally on to the ligamentum nuchae.

In our specimen of *Tupaia*, in the two described by Le Gros Clark (1926) and in *Galago* (Murie and Mivart 1872), m. rhomboideus was undivided.

The caudal part of m. rhomboideus arose from the lower part of the ligamentum nuchae and from the upper thoracic spines. Variations in its caudal limit are summarized in Table 21.

The direction and insertion of the muscle were as in other Primates.

In our specimen of *Tupaia*, in the two described by Le Gros Clark (1924) and in four of *Ptilocercus* (Le Gros Clark 1926) a fleshy bundle arose from the lateral mass of the atlas and passed caudally to insert into the medial end of the scapular spine forming a discrete m. atlantoscapularis posterior.

(b) *hangers:* (Pl. 9, fig. 40 and Pl. 10, fig. 44) : In *Nycticebus* and *Perodicticus*, the cranial part of m. rhomboideus was a small slip arising from the external occipital protuberance only, and separated from the more caudal part by a triangular gap containing loose areolar tissue. In *Propithecus*, the origin of m. rhomboideus extended cranially to the occipital bone. Edwards and Grandidier (1875) reported a similar finding in this genus, and Mivart and Murie (1865) reported a corresponding condition in *Nycticebus*.

The caudal part of m. rhomboideus took origin from the lower part of the ligamentum nuchae and the upper thoracic vertebrae, the caudal limit usually being the spine of the fifth (Table 21).

The direction of the fibres and their method of insertion conformed to the typical primate pattern.

TABLE 21
Variation in the origin of *m. rhomboideus* (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which the caudal limit of origin was from the spines of			
	Present study	Literature*	T.3	T.4	T.5	T.6
Quadrupeds ..	6	19	16.0	48.0	36.0	—
Hangers ..	4	9	15.4	7.7	69.2	7.7

Significance of difference in mean caudal limit of origin of *m. rhomboideus* : Quadrupeds and Hangers : $P=0.1-0.05$.

Locomotor group	Number of specimens		Percentage of cases in which segments were spanned									
	Present study	Literature*	4	5	6	7	8	9	10	11	12	
Quadrupeds ..	6	19	16.0	—	20.0	—	8.0	32.0	16.0	—	8.0	
Hangers ..	4	6	—	10.0	40.0	10.0	20.0	20.0	—	—	—	

Significance of difference in mean numbers of vertebral spines spanned by *m. rhomboideus* : Quadrupeds and Hangers : $P=0.2-0.1$.

* Clark 1924, 1926 ; Miller 1943 ; Mivart & Murie 1865 ; Murie & Mivart 1872 ; Schuck 1913 ; Woollard 1925.

M. serratus magnus pars cranialis

General description: The general configuration of *m. serratus magnus pars cranialis* (p. 592) is similar in both the Prosimii and Anthropoidea.

Principal contrasts between locomotor groups: (Pls. 9, 10 and Table 22) : Recorded variations of this muscle appear not to correlate with the locomotor groupings.

Variation: (a) *quadrupeds:* The muscle had a continuous origin from all the cervical transverse processes and from certain upper ribs. Recorded variations in the numbers of segments spanned are summarized in Table 22. In eight specimens from the genera *Ptilocercus* (Le Gros Clark 1926), *Tupaia* (Le Gros Clark 1924), *Lemur* (Schuck 1913) and *Tarsius* (Woollard 1925), the muscle was divided near its midpoint by loose areolar tissue.

The direction of the fibres and their method of insertion agreed with the common primate pattern.

(b) *hangers:* (Pl. 9, fig. 40 and Pl. 10, fig. 44) : *M. serratus magnus pars cranialis* took continuous origin as in quadrupeds from the cervical transverse processes and the upper ribs. Variations in the numbers of segments spanned are summarized in Table 22.

In our specimen of *Propithecus* and in three specimens of *Nycticebus* described by Miller (1943), the muscle was divided near its midpoint by a narrow band of loose areolar tissue. In a further specimen of *Nycticebus* described by Schuck (1913) the muscle was divided by two equally spaced bands.

The direction and insertion of the fibres were similar to those characteristic of the Primates as a whole.

TABLE 22
Variation in the origin of *m. serratus magnus pars cranialis* (Prosimii).

Locomotor group	Number of specimens		Percentage of cases in which		
	Present study	Literature*	9	10 segments were spanned	11
Quadrupeds ..	6	3	—	88.9	11.1
Hangers ..	4	8	58.3	33.3	8.3

Significance of difference in mean numbers of segments spanned by *m. serratus magnus pars cranialis* : Quadrupeds and Hangers : $P=0.02-0.01$.

* Clark 1924 ; Huntington 1897 ; Miller 1943 ; Schuck 1913 ; Woollard 1925.

M. subclavius

General description: In Prosimii, the main features of *m. subclavius* are similar to those found in the Anthropoidea (p. 593) except that the origin is restricted to the first costal cartilage and does not involve the rib. The muscle is inserted into the intermediate third of the clavicle.

Principal contrasts between locomotor groups: (Pls. 8-10) : The general form of *m. subclavius* appears similar in quadrupeds and hangers.

Variation: (Pl. 8, fig. 34 ; Pl. 9, fig. 38 and Pl. 10, fig. 42) : Within each locomotor group, the characters of *m. subclavius* were constant.

M. omohyoideus

General description: The main features of *m. omohyoideus* correspond with those described for the Anthropoidea (p. 595).

Principal contrasts between locomotor groups: (Pls. 8-10) : The variations in this muscle showed no correlations with the locomotor groups.

Variation: (a) *quadrupeds*: (Pl. 8, fig. 34) : The origin and fibre direction of this muscle showed no variation.

In our specimen of *Tupaia*, and in seven specimens of *Ptilocercus*, *Tarsius* and *Lemur* (Le Gros Clark 1926, Woollard 1925, Parsons 1898), *m. omohyoideus* comprised two bellies joined by an intermediate tendon.

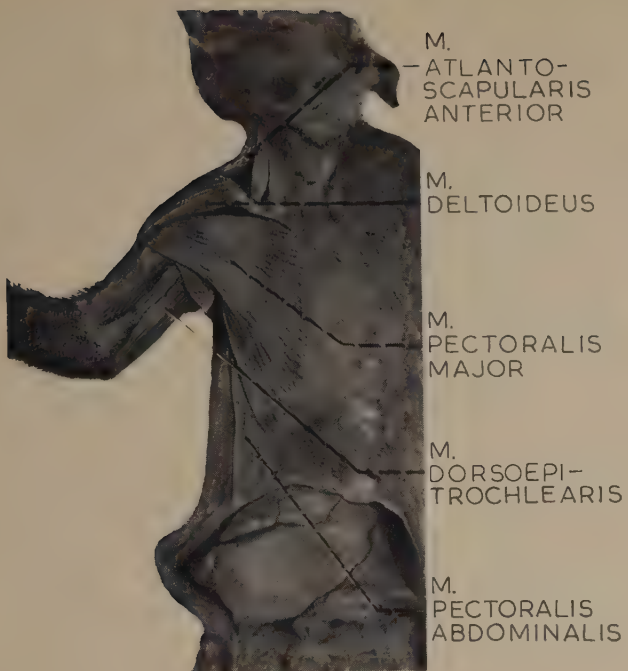
The muscle was usually inserted into the superior angle of the scapula, but in *Tupaia* and in the four specimens of *Ptilocercus* described by Le Gros Clark (1926), the muscle inserted into the base of the coracoid process.

(b) *hangers*: (Pl. 9, fig. 38 and Pl. 10, fig. 42) : The origin, direction and insertion of *m. omohyoideus* showed no noteworthy variations. Although the muscle is normally undivided, there was an intermediate tendon in specimens of *Nycticebus* and *Propithecus* described by Mivart and Murie (1865) and by Hill (1953).

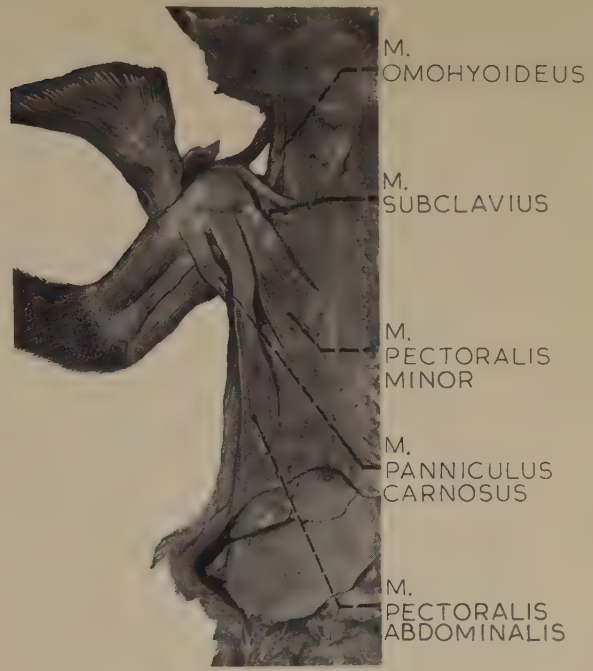
PLATE 8

PLATE 8

Figs. 33-36 The shoulder muscles of a quadrupedal prosimian—*Tupaia sp.*

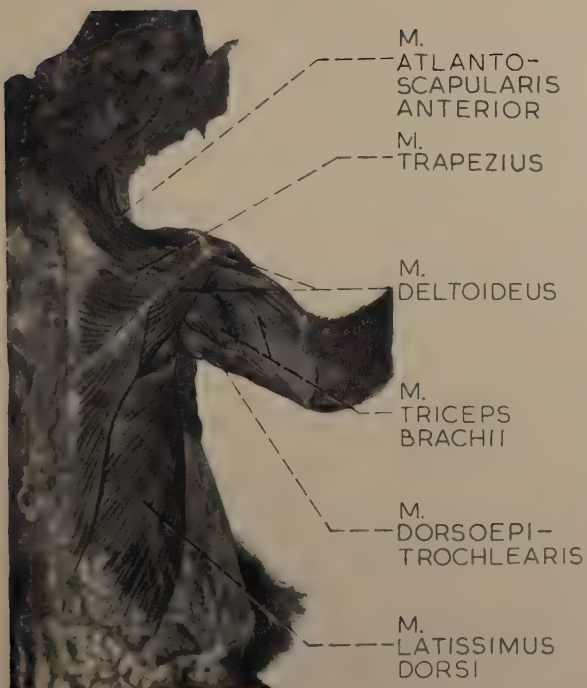


33

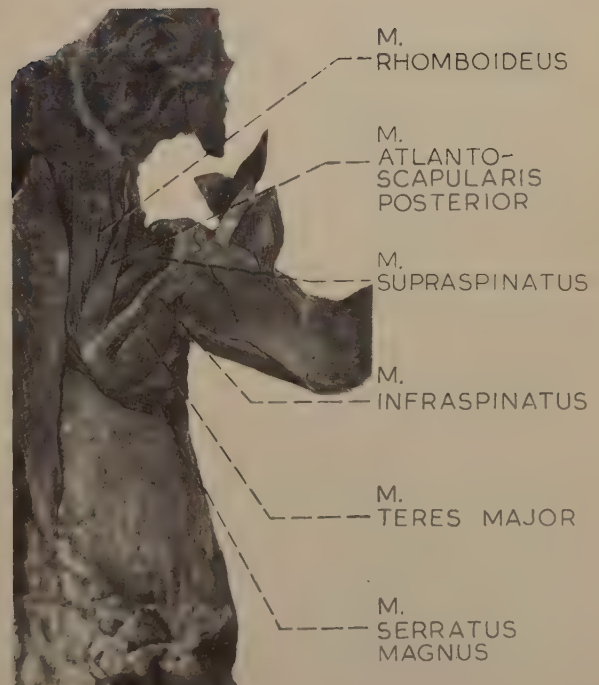


34

5 CENTIMETRES



35



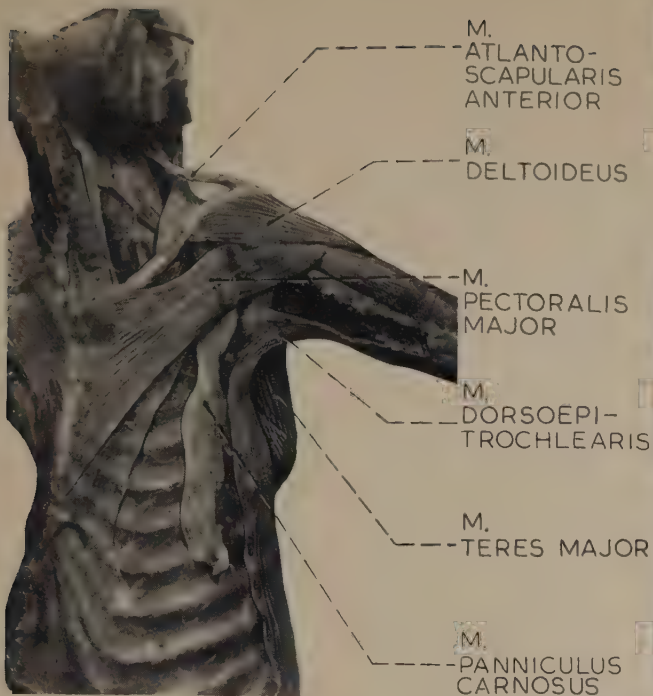
36

Figs. 33-36. The shoulder muscles of a quadrupedal prosimian—*Tupaia* sp.

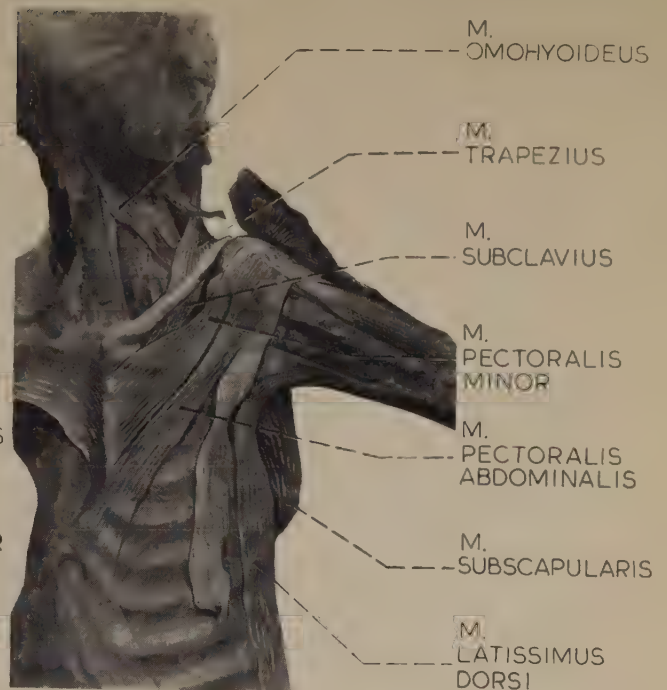
PLATE 9

PLATE 9

Figs. 37-40 The shoulder muscles of a prosimian hanger (lorisiformes)—*Nycticebus sp.*



37

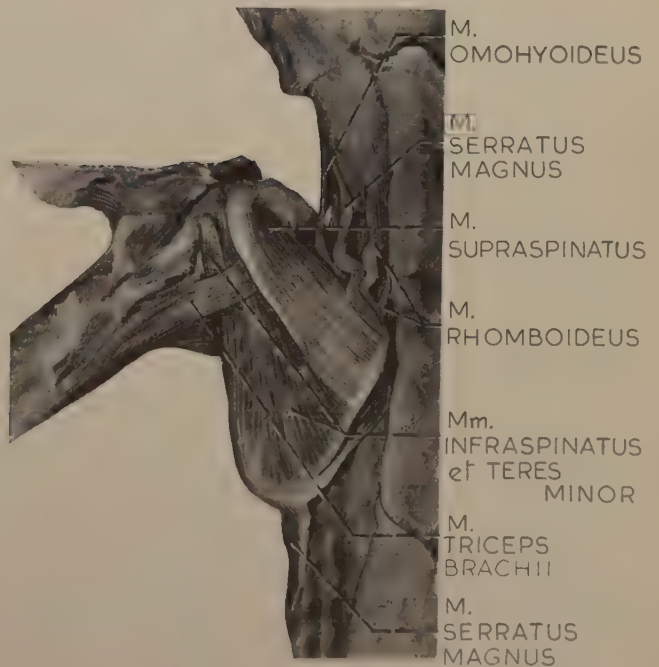


38

5 CENTIMETRES



39



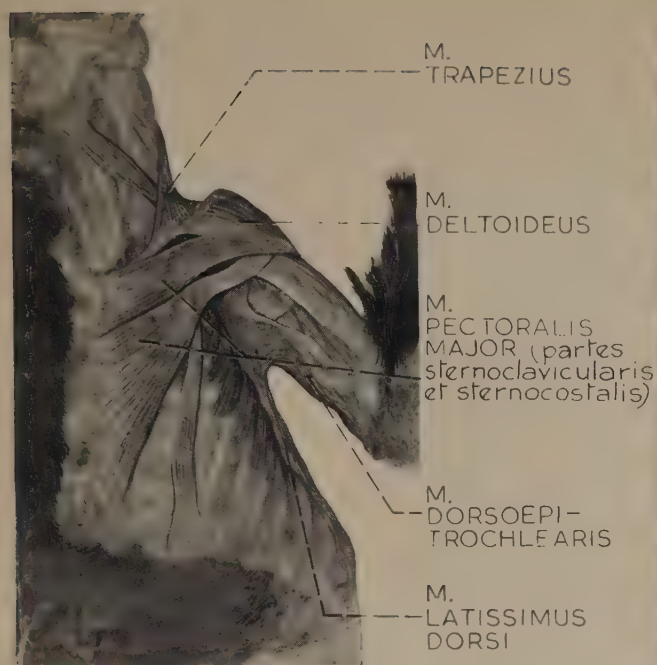
40

Figs. 37-40. The shoulder muscles of a prosimian hanger (lorisiformes)—*Nycticebus* sp.

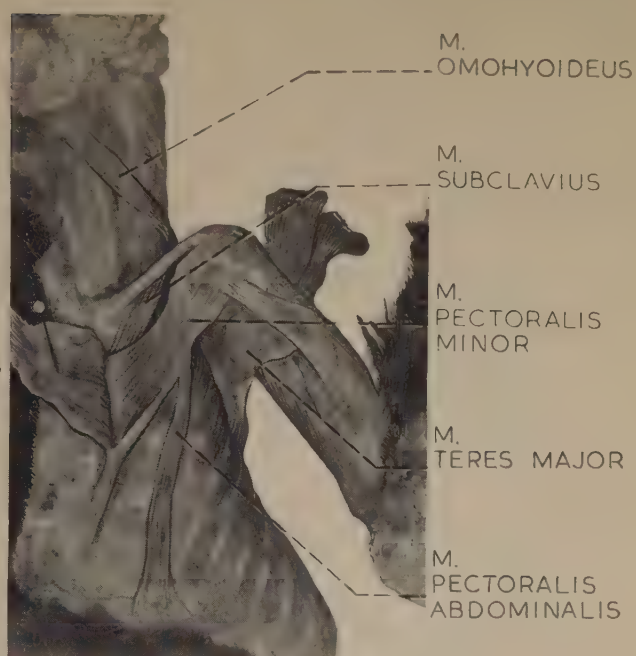
PLATE 10

PLATE 10

Figs. 41-44 The shoulder muscles of a prosimian hanger (lemuriformes)—*Propithecus sp.*

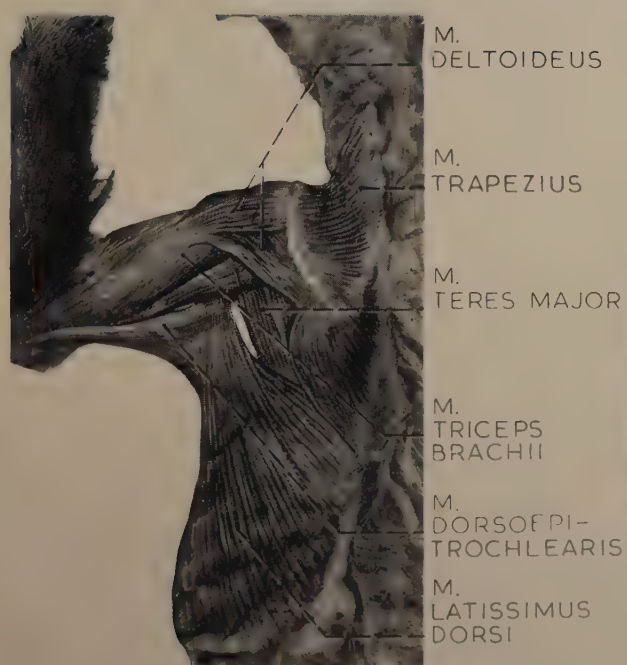


41

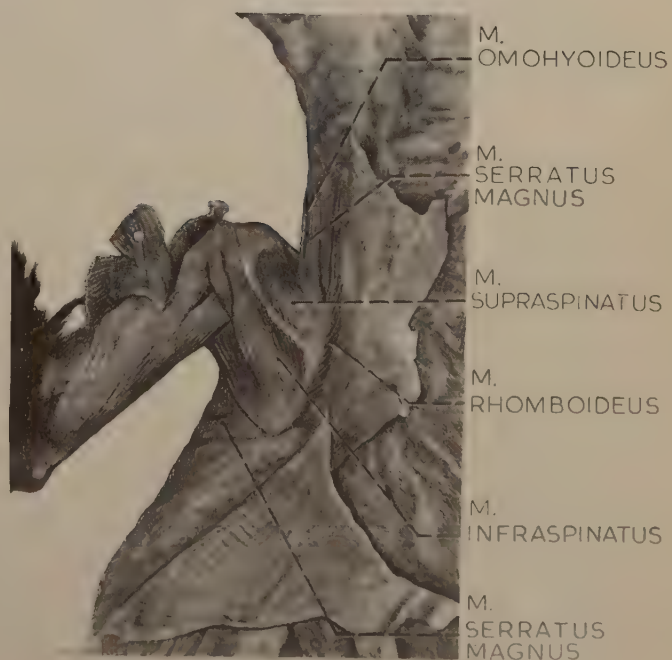


42

5 CENTIMETRES



43



44

Figs. 41-44. The shoulder muscles of a prosimian hanger (lemuriformes)—*Propithecus* sp.

Statistical study
(PROSIMII)

Tables

Basic statistical data relating to (a) quadrupeds and (b) hangers are presented in Table 23 in which is also recorded the significance of the differences between corresponding mean values. As in the Anthropoidea, ratios between on the one hand, the weights of either the propulsive or arm-raising units and, on the other, the fixers of the shoulder joint and scapula, provide a measure of the "relative size" of the various functional units.

TABLE 23
Relative weights of shoulder muscles (Prosimii).

	QUADRUPEDS			HANGERS		
	Mean	Number of specimens	S.E. of mean	Mean	Number of specimens	S.E. of mean
Propulsive muscles/fixers of shoulder joint and scapula	130.7	5	15.43	102.0	4	11.21
Pectoral mass/fixers of shoulder joint and scapula	59.4	5	5.14	36.3	4	3.51
M. latissimus dorsi + m. teres major/fixers of shoulder joint and scapula ..	71.3	5	10.70	65.6	4	8.28
Pectoral mass/m. latissimus dorsi + m. teres major	86.3	5	6.36	56.5	4	4.00
Arm raisers/fixers of shoulder joint and scapula	51.3	5	3.35	83.6	4	7.15
M. deltoideus/fixers of shoulder joint and scapula	17.2	5	2.46	26.2	4	6.60
M. trapezius + m. atlantoscapularis anterior + m. serratus magnus pars caudalis/fixers of shoulder joint and scapula	34.1	5	2.78	57.4	4	6.81
M. deltoideus/m. trapezius + m. atlantoscapularis anterior + m. serratus magnus pars caudalis	52.6	5	11.05	49.4	4	16.70
M. trapezius + m. atlantoscapularis anterior/fixers of shoulder joint and scapula	22.1	5	1.79	34.8	4	5.81
M. serratus magnus pars caudalis/fixers of shoulder joint and scapula ..	12.0	5	1.14	22.6	4	1.59
M. trapezius + m. atlantoscapularis anterior/m. serratus magnus pars caudalis	186.4	5	10.67	152.6	4	20.89
Propulsive muscles/arm raisers ..	251.8	5	11.81	121.3	4	3.96

Muscles responsible for propulsion

The propulsive muscles are somewhat bigger in quadrupeds than in hangers although the data are inadequate to establish whether or not this difference is due to factors other than chance. It results from the pectoral mass being significantly bigger in quadrupeds than in hangers, while the relative size of *m. latissimus dorsi* plus *m. teres major* is constant. These findings are corroborated by the observation that the ratio between the weight of the pectoral mass and that of *m. latissimus dorsi* plus *m. teres major* is significantly bigger in quadrupeds than in hangers.

Muscles responsible for raising the arm

The muscles responsible for raising the arm are relatively bigger in hangers than in quadrupeds.

A corresponding trend emerges when each of the main components of the group [first, abductors of the humerus, i.e. *m. deltoideus*; and secondly, muscles responsible for rotating the scapula, i.e. (a) *m. trapezius* together with *m. atlantoscapularis* anterior, (b) *m. serratus magnus pars caudalis*] is considered separately.

The ratio of weights of these two muscular subgroups is similar in both quadrupeds and hangers—a finding that indicates that in hangers, each is enlarged to an equivalent extent.

Each arm of the force couple responsible for scapular rotation [(a) *m. trapezius* together with *m. atlantoscapularis* anterior and (b) *m. serratus magnus pars caudalis*] tends also to be bigger in hangers than in quadrupeds. The finding that the ratio between the two arms is, so far as can be judged from the available data, constant, indicates that, in hangers, they are equally enlarged.

Comparison between propulsive muscles and arm-raisers

The ratio between the weights of, on the one hand, the propulsive muscles, and, on the other, the arm-raising muscles, is significantly bigger in quadrupeds than in hangers. This reflects the findings that in quadrupeds, the propulsive muscles tend to be relatively bigger than in hangers, while the arm-raisers are significantly smaller.

DISCUSSION

The present study has confirmed that variation in the primate shoulder muscles can be classified into firstly “taxonomic” characters which appear to have little mechanical significance, and secondly “adaptive” differences that can be related to contrasts in shoulder function.

The taxonomic characters are of minor significance, but as they are principally meristic, it is to this type of feature that attention has often been drawn in published descriptions of individual primate species. Such characters may be of an “all or

none" nature. Thus, contiguous muscle bundles of *m. deltoideus* and *m. pectoralis major* were fused in all Prosimii, but in none of the Anthropeoidea. Again, *m. atlantoscaphularis posterior* was found constantly in the Tupaiodea but never in the Lemuroidea. At the specific level, the insertion of *m. pectoralis minor* was restricted constantly to the capsule of the shoulder joint in *Macaca mulatta* but extended to neighbouring structures in *M. cyclopsis*.

The characters may, however, appear in both taxonomic groups but with different frequencies. Thus, while interchange of fibres between *m. latissimus dorsi* and *m. teres major* was found in only four per cent. of the Ceboidea, it occurred in fifty-five per cent of the Cercopithecoidea. Again, *m. atlantoscaphularis anterior* lay superficial to *m. trapezius* in thirteen per cent only of the Cebinae but in ninety-two per cent of the Atelinae.

The information in the literature, together with that derived from the present study, has enabled nineteen of these differences between taxonomic groups (Table 24) to be established as statistically significant ($P < 0.05$). It has, however, been exceptional for sufficient data to be available to enable individual species or genera to be compared, and the precise frequencies of occurrence may, in some instances, have been distorted because some sub-divisions of each taxonomic group were not represented in the sample.

But the main variations to which the present study directs attention are those affecting muscular size, form and disposition. The anatomical peculiarity of these contrasts lies in the fact that many transcend the bounds of the customary taxonomic groupings and correlate with locomotor subdivisions. The mechanical significance of these differences cannot be assessed critically until adequate comparative electromyographic studies have been undertaken, but meanwhile, morphological analysis indicates many functional relationships with the locomotor mechanisms.

Both in quadrupedal movement and in brachiation, the body is propelled forwards by retraction of the forelimb, the hand being fixed on the locomotor surface. This movement is then followed, as a preparation for the next propulsive stroke, by protraction of the forelimb, the hand being free. But in brachiators, locomotion is carried out mainly by the strongly-developed forelimb by which the body is suspended, while in quadrupeds, progression is shared by both fore and hind limbs and the body weight is supported from below. In brachiators, therefore, the retraction of the forelimb—i.e. its "power" stroke—results in the propulsion of a greater part of the body weight than in quadrupeds. The movement also starts from a higher initial position, and the main propulsive effort occurs earlier in retraction. Again, while in brachiators, scapular movements are largely rotary, in quadrupeds, they are predominantly linear.

The finding that the overall mass of the propulsive muscles is relatively bigger in brachiators, correlates with the fact that, in this group, the forelimb is almost exclusively responsible for propulsion. This contrast in relative mass mainly affects *m. latissimus dorsi* which is also more cranially directed in brachiators. When, therefore, the limb is in its initial high position, it inserts into the humerus at a wider angle than would be the case were the muscle obliquely disposed as in quadrupeds. In brachiators, therefore, it has a greater mechanical advantage in

TABLE 24
Taxonomic variations in shoulder muscles

Taxonomic level of comparison	Anatomical features	Comparison between						Significance of difference (P)
		Taxonomic group	Number of specimens	Percentage frequency	Taxonomic group	Number of specimens	Percentage frequency	
Subordinal	Fusion of m. deltoideus and m. pectoralis major	Prosimii	28	100.0	Anthropoidea	125	0.0	<0.001
	Fusion of m. pectoralis major and m. pectoralis minor	Prosimii	42	19.0	Anthropoidea	125	0.0	<0.001
	Reduplicated origin of m. dorsoepitrochlearis	Prosimii	36	11.1	Anthropoidea	126	0.0	0.01-0.001
	Presence of m. atlantoscaphularis posterior	Tupaioidea	7	100.0	Lemuroidea	9	0.0	<0.001
	Absence of pars spinalis of m. deltoideus	Tupaioidea	7	85.7	Lemuroidea	7	0.0	0.01-0.001
Superfamilial	Presence of separate occipital head of m. rhomboideus	Tupaioidea	7	0.0	Lemuroidea	9	88.9	0.01-0.001
	Absence of intermediate tendon in m. omohyoideus	Tupaioidea	7	28.6	Lemuroidea	13	84.6	0.05-0.02
	Division of m. serratus magnus pars cranialis	Ceboidea	67	4.5	Cercopithecoidea	32	100.0	<0.001
	Interchange of fibres between m. latissimus dorsi and m. teres major	Ceboidea	56	3.6	Cercopithecoidea	33	54.5	<0.001
	Presence of separate occipital head of m. rhomboideus	Ceboidea	53	58.5	Cercopithecoidea	34	11.8	<0.001
	Presence of m. pectoralis abdominalis	Hominoidea	47	0.0	{ Ceboidea	38	100.0	<0.001
	Origin of m. pectoralis minor from costal cartilages and sternbrae	Hominoidea	150	0.0	{ Cercopithecoidea	37	100.0	<0.001
	Differentiation of m. levator scapulae	Hominoidea	59	98.3	{ Ceboidea	46	100.0	<0.001
					{ Cercopithecoidea	64	100.0	<0.001
					{ Ceboidea	81	1.2	<0.001
Familial	Restriction of insertion of m. pectoralis minor to capsule of shoulder joint	Cebidae	32	3.1	Callithricidae	30	96.7	<0.001
	Division of m. pectoralis major into three parts	Pongidae	46	100.0	Hominae	61	19.7	<0.001
Subfamilial	M. atlantoscaphularis anterior superficial to m. trapezius	Cebinae	8	12.5	Atelinae	12	91.7	0.01-0.001
Generic	Restriction of insertion of m. pectoralis minor to coracoid	Pan	29	24.1	{ Gorilla	16	100.0	<0.001
	Absence of intermediate tendon in m. omohyoideus	Pongo	7	71.4	{ Pongo	8	75.0	0.05-0.02
Specific	Restriction of insertion of m. pectoralis minor to capsule of shoulder joint	Macaca mulatta	14	100.0	Pan	7	0.0	0.05-0.02
					Macaca cyclopsis	50	0.0	<0.001

the earlier stages of retracting the forelimb from the raised position. In quadrupeds, on the other hand, where the limb remains in a low position, the oblique disposition of *m. latissimus dorsi* results in a wider angle of insertion when the forelimb is already partly retracted—its action being therefore more effective during the later phases of retraction.

Again, in brachiators, the transverse orientation of the pectoral mass apparent when the animal is in the "anatomical position", would appear to give the minimum hindrance to extreme arm-raising. But when the arm is fully raised, the orientation of the pectoral mass becomes approximately vertical, and the muscles are, therefore, in common with *m. latissimus dorsi*, in the best position for retracting the arm. In brachiators, further advantage in retraction is provided by the pronounced twist of *m. pectoralis major* which results in a wider angle of insertion of its caudal fibres when the arm is fully raised. In quadrupeds, on the other hand, the relatively cranial direction of the pectoral mass, which remains approximately constant throughout the propulsive stroke, provides efficient retraction from a lower initial position of the forelimb.

The more extensive development in brachiators of the group of arm-raising muscles correlates with the observation that, owing to the more massive proportions of the forelimb and the fact that the movement takes place more directly against gravity, the power of the return movement is greater. Conversely, the weak development of the arm-raising muscles in quadrupeds is consistent with the observation that in this group, the forelimb is smaller and the return movement is partly aided by gravity. The detailed findings that, in brachiators, *m. deltoideus* is big, its three heads form more of a single unit and insert relatively lower on the humerus, are all consistent with the greater power of protraction of the humerus on the limb girdle that is associated with the higher initial position of the forelimb.

In brachiators, the greater relative mass of *m. trapezius*, the more lateral direction of its fibres, their extensive insertion on to the lateral half of the limb girdle and the corresponding configuration of *m. atlantoscapularis anterior*, all increase the efficiency of cranial rotation of the scapula during arm-raising. In quadrupeds, the more cranial direction of *m. trapezius* and its insertion into the whole length of the scapular spine make it a more efficient protractor than rotator—protraction being the more dominant movement during quadrupedal locomotion. The powerful digitations of *m. serratus magnus* which converge upon the caudal angle of the scapula and form a force couple with the correspondingly-developed cranial fibres of *m. trapezius*, also facilitate rotation of the limb girdle of brachiators.

In brachiators, certain features of the propulsive and arm-raising muscles can be regarded as increasing the efficiency of the mechanism for transmitting the trunk weight to the arm when the animal is suspended. Among these, attention may be drawn to the powerfully-developed ventral fibres of *m. latissimus dorsi* which, when the arm is raised, lie almost vertically and transmit weight from the ilium and thoracic cage directly to the arm. Again, during suspension, the thick caudal digitations of *m. serratus magnus* are almost vertical and transmit weight from the lower part of the trunk to the scapula, while the heavily-developed cranial fibres of *m. trapezius* pass cranio-laterally and transmit the weight of the upper

part of the trunk to the shoulder girdle. Finally, the powerfully-developed m. deltoideus lies vertically during suspension, and along with the short scapular muscles provides a mechanism for transmitting weight from the shoulder girdle to the humerus.

In semibrachiators, whose pattern of locomotion is sometimes quadrupedal and sometimes like that of brachiators, the intermediate size, form and disposition of most of the muscles concerned with propulsion, arm-raising and suspension, provides an anatomical compromise between mechanisms specifically adapted for either system of movement.

The use of the human forelimb for purposes other than locomotion is associated with a unique arrangement of the shoulder muscles, some of whose features are like those of brachiators, while others resemble those of quadrupeds. Thus, while the relative power of the propulsive muscles (as reflected in their total mass and in the orientation and proportions of m. latissimus dorsi) are as in quadrupeds, the configuration of the pectoral mass is similar to that in brachiators and the arm can therefore be easily retracted from any raised position. The transversely orientated pectoral muscles also provide a strong flexor of the arm from the anatomical position—this being frequently approximated by man, but seldom by the apes. Again, as a result of the peculiar characters of the arm-raising muscles (m. deltoideus being as big and inserting almost as far down the humerus as in brachiators; the cranial part of m. trapezius and the caudal part of m. serratus anterior being almost as big as in this group, but in form and disposition, resembling quadrupeds), the human arm can be raised as freely as that of brachiators but without the power that in this group is associated both with the increased mass of the forelimb and with the frequency of arm-raising. Another interpretation of the “quadrupedal” configuration of m. latissimus dorsi, the caudal part of m. serratus magnus and the cranial part of m. trapezius, is that the human shoulder lacks those suspensory adaptations seen in brachiators and semibrachiators. The pattern of the musculature of the human shoulder would, therefore, appear to provide a more balanced overall mobility than in monkeys and apes.

In quadrupedal Prosimii, locomotion is similar to that of quadrupedal members of the Anthropeidea, and a striking similarity exists in the form and proportions of the musculature of the two groups. But marked variation occurs in the locomotor mechanisms of different prosimian hangers, hence, parallels with brachiation are less obvious. Thus, in *Perodicticus*, the relatively small arm is not habitually raised so completely as in brachiators, while the hind limb plays a relatively more important part in locomotion; in *Propithecus*, the forelimb is short and appears to make little contribution to the power stroke. Nevertheless, there are several striking similarities in the configuration of the shoulder muscles of brachiators among the Anthropeidea and of hangers among the Prosimii. Thus, in each group, there is a strong development of the ventral edge of m. latissimus dorsi linking the trunk with the arm—in fact, in *Propithecus* this is so prominent as to raise a fold of skin resembling a patagium. Again, in each group, the shoulder girdle is linked with the trunk by the prominent caudal part of m. serratus magnus together with the strong cranial part of m. trapezius, while a relatively powerful m. deltoideus links the shoulder girdle to the arm.

Mention has already been made of how, in brachiators, these features can be regarded as providing a suspensory mechanism, and in prosimian hangers also, the forelimb plays a greater or lesser part in suspending the body. That is, as in brachiators, it is subject to predominantly tensile forces, and to this factor parallels in muscular configuration can most readily be related.

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SUMMARY

(1) A statistical study has been made of qualitative and quantitative features of the shoulder muscles in fifty-two Primates, representing twenty-two genera from the Anthropeoidea and six genera from the Prosimii.

(2) In quadrupedal monkeys from both the Ceboidea (e.g. *Saimiri*) and from the Cercopithecoidea (e.g. *Papio*, *Cercopithecus*) :

- (a) the pectoral muscles are big and are directed cranially ;
- (b) m. latissimus dorsi is thin, its origin is confined to the dorsum of the trunk and its fibres pass obliquely ;
- (c) m. deltoideus is relatively small, and inserts above the mid-point of the humerus ;
- (d) m. trapezius is uniformly thin, most of its fibres are directed caudally and insert into the whole length of the scapular spine ;
- (e) the caudal digitations of m. serratus magnus are few and are scarcely more strongly developed than in the cranial part of the muscle.

(3) In brachiators (*Hylobates*, *Symphalangus*, *Pongo*, *Pan* and *Gorilla*) :

- (a) the pectoral muscles are relatively small and are directed laterally ;
- (b) m. latissimus dorsi is strong, its origin extends towards the ventral aspect of the trunk and its fibres are directly cranially ;
- (c) m. deltoideus is big and inserts below the mid-point of the humerus ;
- (d) the upper fibres of m. trapezius are strongly developed, they are directed laterally and insert only into the lateral parts of the shoulder girdle ;
- (e) the caudal digitations of m. serratus magnus are more numerous than in quadrupeds and are much bigger than those in the cranial part of the muscle.

(4) The morphological features of the short muscles that stabilize the shoulder joint (m. supraspinatus, m. infraspinatus, m. teres minor and m. subscapularis) and of those responsible for stabilizing the shoulder girdle (m. rhomboideus, the

cranial part of *m. serratus magnus*, *m. omohyoideus* and *m. subclavius*) are similar in quadrupeds and brachiators.

(5) In species of New World monkeys (e.g. *Ateles*, *Alouatta*) and Old World monkeys (e.g. *Colobus*, *Nasalis*) which although sometimes moving quadrupedally, often also use the forelimb for reaching above the head and suspending the body, the characters of the propulsive muscles (pectoral musculature and *m. latissimus dorsi*) and of the arm-raising muscles (*m. deltoideus*, *m. trapezius* and the caudal part of *m. serratus magnus*) are intermediate between those found in quadrupeds and brachiators.

(6) In man, some features of the shoulder muscles are like those of quadrupeds while others resemble those of brachiators. Thus :

- (a) the pectoral muscles are as big as in quadrupeds but are directed laterally as in brachiators ;
- (b) *m. latissimus dorsi* is, as in quadrupeds, thin, its origin confined to the dorsum of the trunk and its fibres directed obliquely ;
- (c) *m. deltoideus* is big and inserts almost as far down the humerus as in brachiators ;
- (d) *m. trapezius* is, as in quadrupeds, uniformly thin, its fibres are directed caudally and insert into the whole length of the scapular spine ; but the muscle is relatively big as in brachiators ;
- (e) the caudal digitations of *m. serratus magnus* are few as in quadrupeds, but each is relatively big as in brachiators.

(7) It is suggested that, so far as can be inferred from morphological study:

- (a) the configuration of the shoulder muscles in quadrupeds and brachiators provides systems mechanically efficient for each respective type of locomotion ;
- (b) the intermediate characters of these muscles in semibrachiators provide a mechanical compromise between systems adapted either for quadrupedal locomotion or for brachiation, and
- (c) the unique admixture of features in man provides the human shoulder with a more balanced overall mobility than in other primate groups.

(8) In certain Prosimii (e.g. *Tupaia*, *Lemur*, *Galago*), the configuration of the shoulder muscles corresponds with that typical of quadrupedal monkeys.

(9) In the remaining Prosimii (e.g. *Perodicticus*, *Loris*, *Propithecus*), the characters of the shoulder muscles are basically as in brachiators from the Anthroipoidea.

(10) It is suggested that these parallels between the Anthroipoidea and Prosimii can best be related to whether the forelimb is subject mainly to forces of compression or tension.

(11) In addition to such major "adaptive" differences, a number of meristic characters of no obvious mechanical significance contrast between taxonomic groups of equivalent grade within the Primate order.

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